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A Space- and Time-Scale Characterization of Circulation and Mixing over Submarine Banks, with Application to the Northwestern Atlantic Continental Shelf[1]

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Loder, J. W., C. K. Ross, and P. C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

The circulation and mixing over submarine banks is described in terms of integral space and time scales determined from Eulerian and Lagrangian currents. The time scales include the time for vertical diffusion across the pycnocline or water depth, the recirculation times of any residual gyre, and the residence time over the bank. These may be intercompared to obtain a description of a bank's physical regime and compared with the time scales associated with biological processes to identify possible physical–biological linkages. The space scales include the vertical diffusion distance during a time interval and the excursions associated with horizontal current fluctuations. These may be compared with topographically imposed and biologial space scales. The integral-scale characterization is applied to four northwestern Atlantic banks. The data suggest that the vertical diffusion time is longer than the recirculation and residence times of the surface water on Flemish Cap, shorter on Browns and Georges Banks, and comparable with the Southeast Shoal residence time; the recirculation time is greater than the residence time of the near-surface water on all banks except Georges and the western cap of Browns Bank; and the cross-bank excursions are much less than the bank radius on all except Browns Bank.

La circulation et le mélange au-dessus des bancs sous-marins sont décrits en fonction d'échelles intégrales spatio-temporelles déterminées à partir des courants de types eulérien et lagrangien. Les échelles temporelles comprennent la durée de la diffusion verticale au travers de la pycnocline ou de la colonne d'eau, la durée de recirculation de tout tourbillon résiduel et le temps de séjour au-dessus du banc. Ces paramètres peuvent être comparés entre eux pour obtenir une description du régime physique du banc, et comparés avec les échelles temporelles liées aux processus biologiques pour déterminer d'éventuelles relations physiques ou biologiques. Les échelles spatiales comprennent la distance de diffusion verticale pendant un intervalle de temps et les diversions liées aux fluctuations des courants horizontaux. Ces valeurs peuvent être comparées à des échelles spatiales biologiques fonction de la topographie. Une caractérisation d'échelle intégrale est appliquée à quatre bancs du nord-ouest de l'Atlantique. Les données obtenues indiquent que la durée de diffusion verticale est plus longue que la durée de la recirculation et le temps de séjour des eaux de surface au bonnet Flamant, plus courte au-dessus des bancs de Brown et de Georges et comparable au temps de séjour au-dessus des hauts-fonds Sud-est. La durée de la recirculation est plus importante que le temps de séjour des eaux situées près de la surface au-dessus de tous les bancs à l'exception du banc de Georges et de la partie ouest du banc de Brown, et, à l'exception du banc de Brown, les diversions latérales sont de beaucoup inférieures aux rayons des bancs.

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It has been long recognized that the physical environment may have a major influence on biological processes in the ocean (e.g. Hjort 1914; Gran and Braarud 1935; Riley 1942; Sverdrup 1953), but there has been a substantially increased effort during the past decade directed at identifying the specific linkages between marine ecosystems and their environment (see Legendre and Demers 1984 and Shepherd et al. 1984 for recent reviews). An important factor in these linkages is the occurrence of variability in the physical environment on a wide range of space and time scales (e.g. Haury et al. 1978; Harris 1980; Denman and Gargett 1983; Horne and Platt 1984). The spatial structure of environmental variables such as current and temperature may affect the distribution of marine organisms, on scales ranging from metres in the vertical to order 10^4 km in the horizontal. Furthermore, temporal variability on scales ranging from seconds for turbulent fluctuations to years and decades for climatic variations in the atmosphere–ocean system may be important in several ways. In the first place, the biological–physical linkages are likely to involve physical processes with time scales, or which result in environmental changes on time scales, that match the natural time scales of the biological processes. Longer-term variability in the "matched" physical processes may then control the time scales of variability in the affected biological processes and perhaps the entire ecosystem. In addition, it may be necessary to resolve energetic higher-frequency temporal variability to obtain an adequate description of the physical environment, in order to avoid spurious contributions from aliasing.

[1]J. C. Stevenson Memorial Lecture (1988), delivered by J. W. Loder.

A vertical space scale that is imposed on the physical environment in the ocean is the water depth. In many areas the coastline and bathymetry also set horizontal space scales. One such example is the occurrence of submarine banks on the northwestern Atlantic continental shelf off eastern Canada. There are about 20 offshore banks with horizontal scales of order 10^2 km on the Labrador, Newfoundland, Scotian, and New England shelves between Cape Chidley and Cape Cod. Several of these banks are known to be characterized by clockwise residual circulations (e.g. Bigelow 1927; Ross 1980; Petrie and Anderson 1983; Smith 1983) and distinct water masses (e.g. Hopkins and Garfield 1981; Akenhead 1986).

Assuming that the space scales of the physical environment are set, such as by the coastal or submarine morphology, then the understanding of biological–physical interactions may be advanced by determining the "*integral*" *time scales* for specified environmental changes as a result of various processes in the set spatial domain. If the specified changes are in the distribution of passive scalars, for example, then the integral time-scale determination is a form of scale analysis on the various terms in the scalar conservation equation. Examples of such integral scales include the time for mixing a scalar over the extent of the domain (such as the water depth), the time for recirculation in a gyre, and the time for replacement of the waters within the domain. Several applications of a time-scale characterization of the physical environment are immediately apparent. The relative importance of the various components (e.g. vertical versus horizontal) of a region's current regime to scalar transfer may be identified, pointing to directions for further investigation of the physical regime. The relationship of the integral time scales to the time scales of the biological processes may suggest specific hypotheses for biological–physical linkages. Finally, a time-scale characterization of the physical environment may not only be a useful concise description, but it may be an adequate quantitative description for the physical component of some highly aggregated ecosystem models (e.g. Gordon et al. 1986); on the other hand, a more detailed representation of the physical environment will undoubtedly be required in many models (e.g. Klein and Steele 1985).

Alternatively, the physical environment may be characterized in terms of *integral space scales* describing the environmental changes occurring during specified time periods. These periods may be chosen as the time scales of the biological processes, and the associated integral space scales may be compared with the space scales of the submarine topography or biogeography to identify possible physical–biological interactions.

The integral-scale approach is demonstrated here with the derivation of characteristic space and time scales for circulation and mixing on offshore submarine banks. The formalism is applied to four northwestern Atlantic banks which have traditionally supported rich commercial fisheries and have been, or are currently, the focus of investigation for physical oceanographic influences on their biological productivity. The emphasis is on the general approach and its interpretation. However, the application also provides a first intercomparison of the circulation and mixing on these four specific banks which should aid the identification of gaps in the existing physical oceanographic database. It is suggested that the approach and its application may be useful in the evaluation of existing hypotheses for physical oceanographic influences on the biological productivity of these and other submarine banks (e.g. Cohen et al. 1982; Iles and Sinclair 1982; O'Boyle et al. 1984; Frank and Carscadden 1988) and in the identification and quantitative description of environmental contributions to differences in their ecosystems.

In the next section the physical oceanographic settings of the four banks under consideration are described and the data sources briefly summarized. The horizontal current variability on each bank is discussed using the results of statistical analyses of moored current measurements. Then, separate sections are devoted to the derivation and application of three integral time scales for bank circulation and mixing. Next, some integral space scales associated with horizontal current variability are introduced and their magnitudes for the banks presented. The paper concludes with a comparative discussion of the oceanographic regimes on the four banks and suggestions for using the integral-scale approach to examine physical–biological linkages.

Physical Oceanographic Background on Four Northwestern Atlantic Banks

Setting and Information Sources

The four banks to which the space- and time-scale characterization is applied are Flemish Cap, the Southeast Shoal of the Grand Bank, Browns Bank, and Georges Bank (Fig. 1). Estimates of the space scales set by their submarine topography are summarized in Table 1. Note that we are primarily concerned with the shallow plateau of each of these banks so that the spatial domain under consideration is generally only part of the bank's total extent.

Flemish Cap (Fig. 1a) is a relatively large and relatively deep bank situated on an eastward protrusion of the eastern North American continental shelf into the Atlantic Ocean. The early information on its general oceanography was summarized by

TABLE 1. Estimates of topographic space scales for specified domains on the four northwestern Atlantic banks.

	Minimum depth (m)	Isobath taken to define plateau (m)	Average depth of plateau (m)	Horizontal area of plateau ($km^2 \times 10^3$)	Effective radius of plateau (km)
Flemish Cap	126	400	280	28	95
Central cap	126	200	160	5.5	42
Southeast Shoal	36	60	53	19	78
Browns Bank	29	110	91	4.4	37
Western cap	29	70	60	0.6	14
Georges Bank	3	110	61	30	100
Central bank	3	60	40	14	70

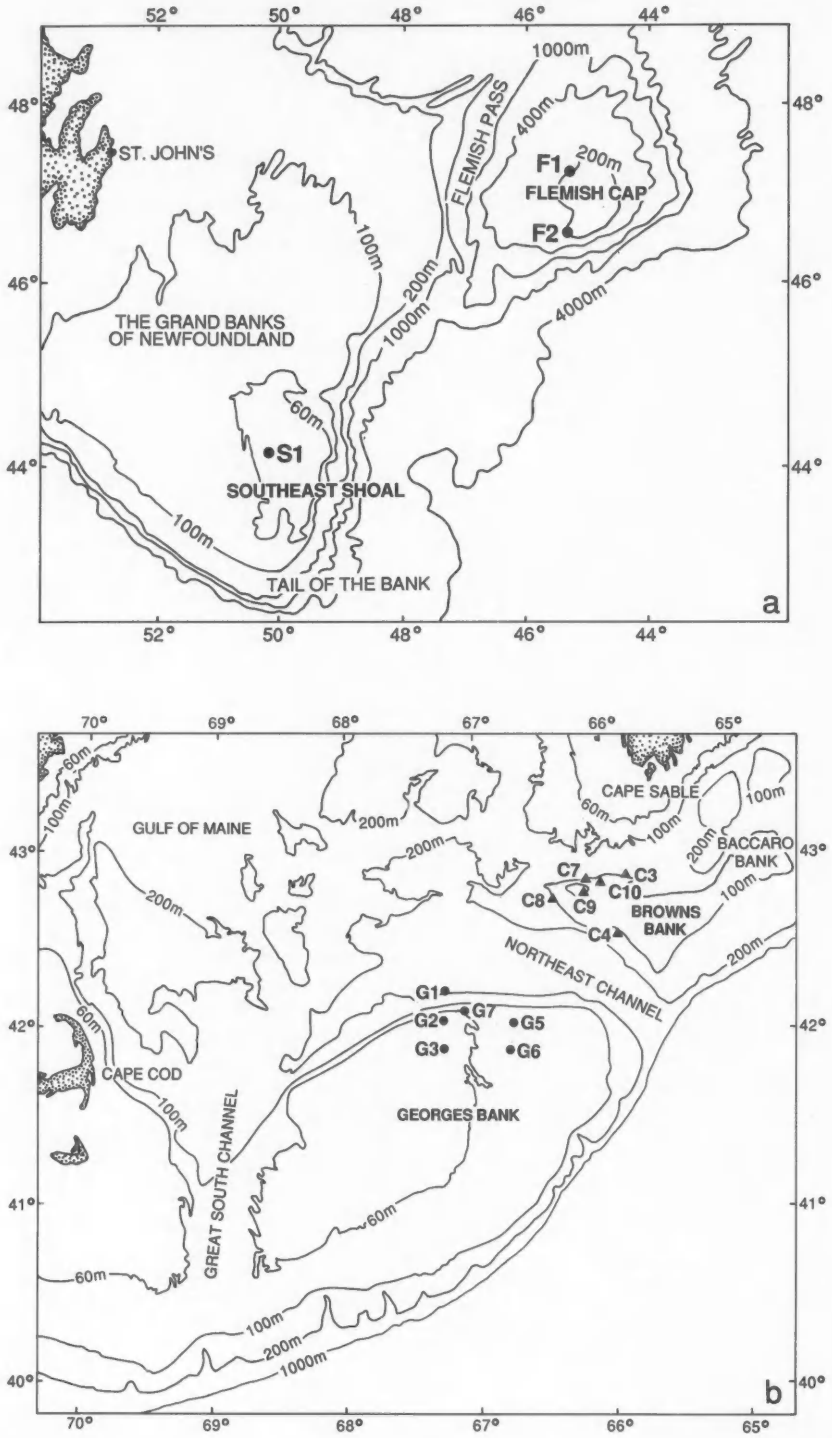

FIG. 1. Bathymetry and moored measurement sites on (a) Flemish Cap and Southeast Shoal and (b) Browns and Georges Banks.

Templeman (1976) and Hayes et al. (1977), in preparation for a major international field investigation of environmental influences on the year-class strengths of cod and redfish: the Flemish Cap International Experiment (Akenhead 1978; Lilly 1986). The experiment's physical oceanographic component included moored current measurements at two sites (F1, F2) on the Cap during January–July 1979 (Ross 1980; instruments at two other sites were not recovered) and the release of six satellite-tracked drogued buoys (Ross 1981). The moored and drifter observations and geostrophic computations (e.g. Kudlo et al. 1984) support the earlier suggestions that the mean circulation in the region is strongly influenced by a branch of the Labrador Current flowing eastward across the northern side of the Cap and then southward on its eastern side, contributing to a weak clockwise gyre over the Cap's plateau.

The Southeast Shoal (Fig. 1a) is the shallowest portion of the extensive Grand Bank. Information on its circulation has come primarily from geostrophic calculations (Smith et al. 1937; Kudlo et al. 1980) which suggest that there is also a weak clockwise circulation in this area in summer (also see Petrie and Anderson 1983). In 1986 and 1987 the Shoal was the site of more detailed oceanographic field investigations by the Department of Fisheries and Oceans of Canada, including moored current and temperature measurements during the spring–fall period and a study of environmental influences on the abundance and distribution of larval capelin (Frank and Carscadden 1988). The presently available moored current measurements are for the period April–October 1986 at site S1 near the centre of the Shoal.

Browns Bank (Fig. 1b) is an elongated, relatively small bank situated at the western end of the Scotian Shelf along the southeastern boundary of the energetic Gulf of Maine/Bay of Fundy tidal system. Moored current measurements were obtained at two sites (C3, C4) in 1979–80 during the Cape Sable Experiment (Smith 1983), revealing a persistent clockwise gyre. More intensive, physical oceanographic measurements were taken during the period April 1983 – March 1985 (Smith 1988) as part of the Southwest Nova Scotia Fisheries Ecology Program which examined, among other things, environmental influences on the Bank's haddock stock. These measurements included moored observations at four sites (C7, C8, C9, C10) on and around the Bank's western cap, which is the focus of the discussion here, and the release of satellite-tracked drogued buoys.

Georges Bank (Fig. 1b) is a relatively large bank lying along the southern boundary of the Gulf of Maine such that it, too, is strongly influenced by the region's large tides. A number of field investigations into the Bank's circulation have been conducted, dating from Bigelow's (1927) early hydrographic observations to Bumpus and Lauzier's (1965) drifter studies to extensive moored current measurements and drifter studies during the (U.S.A.) New England Outer Continental Shelf Physical Oceanography Program in the late 1970's (Flagg et al. 1982). Other moored current measurements include long-term observations at one location during 1975–79 (Butman and Beardsley 1987), observations at six sites on the northern side of the Bank in the fall of 1978 as part of the international Georges Bank Larval Herring Patch Study (e.g. Lough and Trites 1986), and observations at a single site on the northern side of the Bank in the summer of 1985 during a field study of primary production in relation to the Bank's tidal front (Horne et al. 1988). The early observations revealed a seasonal clockwise gyre over the Bank (see Bumpus 1976 for a review), and the more recent moored measurements indicate that the gyre persists throughout the year but with maximum intensity in late summer (Butman et al. 1982, 1987). We use observations from five of the Patch Study mooring sites (G1, G2, G3, G5, G6) and the 1985 site (G7).

Means and Variances of Moored Current Measurements

A first intercomparison of the magnitudes of the mean and time-varying components of current on the four banks is presented in Tables 2 and 3 which summarize the statistics of the moored measurements under consideration (see Fig. 1 for station locations). The statistical summary in Table 2 has the same format as those in Butman et al. (1982) and Lively (1984, 1985) for other observations from Georges Bank and the southwest Nova Scotia region, respectively, so that further comparison with other sites is possible. The current statistics have been computed in Cartesian co-ordinate systems aligned with the local side of the bank so that the $+y$-axis is directed along-bank (i.e. parallel to the side of the bank) with shallow water to the right and the $+x$-axis is directed cross-bank (i.e. across the side of the bank) towards shallow water. First, a time series with a sampling interval of 1 h was computed for each current component. These "1-h" time series were then low-pass filtered with a 129-point Cartwright filter (>95% power passed at periods >40 h, 50% at 31 h, <1% at periods <24 h) and subsampled every 6 h, yielding "6-h" time series. The means in Table 2 are over the entire length of each 1-h record (up to 7 mo), and standard deviations are presented for both the 1-h (the total standard deviation, σ_1, of each current component) and the 6-h data (the subtidal standard deviation, σ_6). The standard error of each mean is based on the subtidal standard deviation, the record length, and the autocorrelation time scale of the appropriate time series. The current variability statistics are further summarized in Table 3 where the ratios of cross-bank to along-bank standard deviation are presented for both the 1-h and 6-h records, as well as the ratios of subtidal to total standard deviation for the total (vector) currents. The latter, which can also be interpreted as the square root of the ratio of subtidal to total kinetic energy, is taken as

$$\Sigma_6/\Sigma_1 \text{ where } \Sigma_i = \{\sigma_i^2(u) + \sigma_i^2(v)\}^{1/2}.$$

In all cases the mean of the along-bank current component is substantially greater than its standard error (Table 2) and, except for site C9 near the cap of Browns Bank, it is positive (i.e. clockwise) everywhere. The mean of the cross-bank current component is also larger than its standard error in most cases. However, with the exceptions of the Southeast Shoal site and some near-bottom instruments on Browns Bank, the cross-bank mean is much less than the along-bank mean so that the moored observations are consistent with clockwise mean gyres over Flemish Cap and Browns (outside the near-bottom layer) and Georges banks. There are local mean current speeds of up to 0.03, 0.22, and 0.39 $m \cdot s^{-1}$ associated with these respective gyres, although these values are dependent on the locations, seasons, and record lengths of the available observations.

The total standard deviation of each of the two current components (Table 2) is of order 0.1 $m \cdot s^{-1}$ for the Flemish Cap and Southeast Shoal sites and generally in the range 0.2–0.7 $m \cdot s^{-1}$ on Browns and Georges banks where there is a suggestion of an inverse dependence on water depth. The along-bank and cross-bank total standard deviations are of the same order of magnitude (Table 3), although there is generally greater var-

TABLE 2. Locations, times and statistics of moored current measurements from the four northwestern Atlanti
(e.g. F1, S1, etc.), and the mooring number refers to the consecutive mooring deployment of the Bedford
G6 were obtained by the National Marine Fisheries Service, Woods Hole, MA, USA. The statistics are for
the bank (*x*: cross-bank, positive towards shallow water; *y*: along-bank, positive clockwise), and σ_1 and σ_6 a
standard error of the mean (SE) is taken as $\sigma_6/\sqrt{n_b^*}$, where n_b^* is the effective number of degrees of freedo

Site (depth)	Location	Mooring No.	Instr. depth (m)	Start/stop (d·mo·yr)	Duration (d)	*Y*-axis orientation (°T)	*U*(m·s Mean ± SE
Flemish Cap							
F1 (204 m)	47°20.3′N	322	54	11.1.79/16.7.79	186	60	0 ± 0.004
	45°08.5′W		184	11.1.79/9.7.79	178		−0.002 ± 0.003
F2 (205 m)	46°41.0′N	324	185	13.1.79/18.4.79	95	320	−0.011 ± 0.005
	45°10.0′W						
Southeast Shoal							
S1 (55 m)	44°14.4′N	774	20	18.4.86/3.8.86	106	0	−0.023 ± 0.007
	50°04.2′W		45	18.4.86/17.10.86	182		−0.017 ± 0.002
Browns Bank							
C3 (110 m)	42°51.5′N	554	15	8.4.83/6.11.83	212	104	0.051 ± 0.015
	65°51.5′W	590	6	6.11.83/16.3.84	130		0.021 ± 0.016
		554	50	8.4.83/6.11.83	212		0.030 ± 0.009
		590	27	6.11.83/25.5.84	201		0.043 ± 0.011
		590	47	6.11.83/25.5.84	201		0.043 ± 0.010
		554	100	8.4.83/16.4.83	8		−0.052[a]
		590	97	6.11.83/25.5.84	201		−0.094 ± 0.011
C4 (110 m)	42°33.0′N	326	14	27.4.79/7.8.79	102	104	−0.001 ± 0.032
	65°56.0′W	349	9	8.8.79/18.10.79	72		−0.002 ± 0.026
		360	15	18.10.79/12.3.80	146		−0.051 ± 0.009
		383	12	28.3.80/24.8.80	149		0.041 ± 0.018
		326	49	27.4.79/8.8.79	103		−0.010 ± 0.020
		349	46	8.8.79/18.10.79	72		−0.013 ± 0.012
		360	50	18.10.79/28.3.80	162		0.014 ± 0.008
		326	99	27.4.79/8.7.79	72		−0.019 ± 0.009
		349	96	8.8.79/18.10.79	72		−0.006 ± 0.008
		360	100	18.10.79/28.3.80	162		−0.003 ± 0.007
		383	97	28.3.80/24.8.80	148		−0.012 ± 0.007
C7 (115 m)	42°50.9′ N	591	22	4.11.83/25.5.84	203	90	0.058 ± 0.008
	67°09.3′ W		35	6.12.83/25.5.84	171		0.067 ± 0.008
			55	4.11.83/25.5.84	203		0.017 ± 0.006
			105	4.11.83/25.5.84	203		−0.117 ± 0.006
C8 (111 m)	42°42.3′ N	592	16	8.11.83/19.2.84	103	330	−0.027 ± 0.017
	66°24.9′ W		30	8.11.83/24.5.85	198		−0.011 ± 0.008
			100	8.11.83/24.5.85	198		−0.032 ± 0.009
C9 (53 m)	42°46.4′ N	555	14	7.4.83/3.7.83	87	180	0.016 ± 0.011
	66°11.1′ W	593	13	3.11.83/8.12.83	35		−0.021 ± 0.036
		555	39	7.4.83/3.11.83	210		0.045 ± 0.004
		593	38	3.11.83/15.3.84	133		0.028 ± 0.010

Atlantic banks. Each mooring site is identified by a two-symbol code
Bedford Institute of Oceanography. The measurements at sites G5 and
are for right-handed coordinate systems aligned with the local side of
and σ_6 are the total and subtidal standard deviations, respectively. The
f freedom for low-passed data (Bayley and Hammersley 1946).

	U(m·s^{-1})		V(m·s^{-1})		
	σ_1	σ_6	Mean ± SE	σ_1	σ_6
4	0.068	0.045	0.019 ± 0.007	0.068	0.037
3	0.068	0.038	0.022 ± 0.004	0.064	0.030
5	0.087	0.044	0.029 ± 0.009	0.102	0.062
7	0.129	0.030	0.013 ± 0.007	0.109	0.036
2	0.109	0.023	0.016 ± 0.003	0.084	0.029
5	0.175	0.087	0.080 ± 0.015	0.417	0.091
6	0.228	0.138	0.114 ± 0.028	0.462	0.166
9	0.154	0.060	0.117 ± 0.006	0.442	0.059
1	0.218	0.099	0.103 ± 0.023	0.453	0.150
0	0.206	0.087	0.127 ± 0.014	0.454	0.130
	0.178	0.052	0.029[a]	0.339	0.078
1	0.214	0.071	0.067 ± 0.008	0.319	0.087
2	0.283	0.130	0.111 ± 0.018	0.365	0.107
6	0.287	0.125	0.022 ± 0.022	0.400	0.129
9	0.257	0.097	0.082 ± 0.017	0.404	0.160
8	0.254	0.114	0.070 ± 0.018	0.348	0.113
0	0.234	0.063	0.147 ± 0.011	0.366	0.067
2	0.245	0.071	0.152 ± 0.010	0.402	0.083
8	0.240	0.077	0.102 ± 0.012	0.381	0.133
9	0.192	0.041	0.044 ± 0.013	0.251	0.060
8	0.201	0.065	0.043 ± 0.011	0.262	0.066
7	0.199	0.086	0.056 ± 0.012	0.281	0.123
7	0.190	0.046	0.056 ± 0.009	0.302	0.063
8	0.282	0.100	0.224 ± 0.022	0.503	0.148
8	0.277	0.088	0.212 ± 0.015	0.447	0.122
6	0.246	0.077	0.179 ± 0.011	0.406	0.121
6	0.282	0.069	0.148 ± 0.013	0.266	0.101
7	0.244	0.102	0.124 ± 0.021	0.501	0.135
8	0.192	0.072	0.173 ± 0.022	0.465	0.128
9	0.199	0.052	0.044 ± 0.008	0.327	0.065
1	0.446	0.051	−0.048 ± 0.013	0.431	0.056
6	0.492	0.130	−0.077 ± 0.033	0.461	0.166
4	0.398	0.047	−0.008 ± 0.006	0.328	0.040
0	0.397	0.089	−0.016 ± 0.007	0.360	0.083

TABLE 2. (*Concluded*)

Site (depth)	Location	Mooring No.	Instr. depth (m)	Start/stop (d·mo·yr)	Duration (d)	*Y*-axis orientation (°T)	*U*(m·s⁻¹) Mean ± SE	σ
C10 (71 m)	42°48.4′ N	594	16	6.11.83/24.5.84	200	114	−0.005 ± 0.009	0.2
	66°01.9′ W	622	14	23.5.84/16.11.84	146		0.034 ± 0.009	0.2
		667	15	16.11.84/25.5.85	190		0.026 ± 0.008	0.2
		556	32	7.4.83/6.11.83	213		0.046 ± 0.010	0.2
		594	31	6.11.83/24.5.84	200		−0.002 ± 0.006	0.2
		622	28	25.5.84/16.11.84	175		0.027 ± 0.008	0.2
		667	31	16.11.84/25.5.85	190		−0.001 ± 0.005	0.2
		594	61	6.11.83/24.5.84	200		−0.003 ± 0.004	0.1
		622	58	25.5.84/16.11.84	175		−0.020 ± 0.006	0.1
		667	61	16.11.84/20.11.84	4		−0.048[a]	0.2
Georges Bank								
G1 (203 m)	42°12.1′ N	299	30	12.10.78/4.11.78	23	80	0.078 ± 0.010	0.2
	67°15.0′ W		40	12.10.78/4.11.78	23		0.026 ± 0.008	0.1
			75	12.10.78/4.11.78	23		0.034 ± 0.005	0.2
G2 (46 m)	42°02.5′ N	300	14	11.10.78/4.11.78	24	80	0.017 ± 0.003	0.6
	67°15.2′ W		15	11.10.78/4.11.78	24		0.043 ± 0.003	0.7
			30	11.10.78/4.11.78	24		−0.002 ± 0.008	0.6
G3 (46 m)	41°52.6′ N	301	15	11.10.78/4.11.78	24	80	0.014 ± 0.006	0.6
	67°15.2′ W		30	11.10.78/4.11.78	24		0.032 ± 0.004	0.6
G5 (75 m)	42°02.0′ N		19	14.9.78/3.11.78	49	90	0.020 ± 0.007	0.6
	66°40.8′ W		44	14.9.78/3.11.78	49		0.031 ± 0.010	0.5
G6 (75 m)	41°52.6′ N		11	14.9.78/14.11.78	61	90	−0.004 ± 0.005	0.6
	66°41.2′ W		26	14.9.78/14.11.78	61		−0.001 ± 0.003	0.5
			36	14.9.78/12.11.78	60		−0.001 ± 0.003	0.4
G7 (63 m)	42°06.7′ N	717	13	24.7.85/8.8.85	15	90	0.052[a]	0.5
	67°02.1′ W		33	24.7.85/8.8.85	15		0.028[a]	0.5

[a]Records too short to compute SE.

$m \cdot s^{-1}$)		$V(m \cdot s^{-1})$		
σ_1	σ_6	Mean ± SE	σ_1	σ_6
0.292	0.124	0.100 ± 0.017	0.597	0.179
0.285	0.084	0.120 ± 0.015	0.568	0.106
0.276	0.107	0.135 ± 0.014	0.558	0.142
0.243	0.054	0.072 ± 0.006	0.502	0.061
0.252	0.085	0.078 ± 0.013	0.549	0.141
0.236	0.054	0.108 ± 0.008	0.559	0.072
0.229	0.071	0.109 ± 0.010	0.539	0.114
0.179	0.058	0.036 ± 0.008	0.395	0.089
0.164	0.034	0.060 ± 0.006	0.406	0.058
0.212	0.027	0.082[a]	0.379	0.023
0.213	0.039	10.251 ± 0.025	0.355	0.082
0.192	0.036	0.237 ± 0.023	0.342	0.077
0.264	0.024	0.159 ± 0.014	0.251	0.050
0.696	0.017	10.143 ± 0.007	0.367	0.039
0.714	0.016	0.127 ± 0.007	0.302	0.035
0.602	0.022	0.080 ± 0.005	0.277	0.024
0.681	0.025	10.061 ± 0.007	0.385	0.041
0.633	0.018	0.062 ± 0.007	0.342	0.032
0.642	0.045	10.101 ± 0.011	0.502	0.058
0.514	0.034	0.059 ± 0.011	0.399	0.038
0.617	0.037	0.046 ± 0.008	0.494	0.059
0.554	0.029	0.027 ± 0.005	0.458	0.037
0.498	0.027	0.016 ± 0.004	0.430	0.030
0.563	0.041	0.385[a]	0.370	0.074
0.541	0.033	0.303[a]	0.327	0.033

TABLE 3. Summary of ratios of cross-bank to along-bank current standard deviations for total ($\sigma_t(u)/\sigma_t(v)$) and subtidal ($\sigma_s(u)/\sigma_s(v)$) variability and ratios of subtidal to total standard deviations [Σ_s/Σ_t] for total (vector) currents at the moored measurement sites of Table 2. The individual record ratios have been grouped and averaged by vertical position (near-surface (N-S), within 25 m of sea surface; near-bottom (N-B), within 25 m of seafloor; middepth (M-D), outside near-surface and near-bottom regions) and, for Browns Bank where there are observations from more than one year, by season (summer (S) for spring to fall deployments and winter (W) for fall to spring deployments).

	$\sigma_t(u)/\sigma_t(v)$			$\sigma_s(u)/\sigma_s(v)$			Σ_s/Σ_t		
Site (depth)	N-S	M-D	N-B	N-S	M-D	N-B	N-S	M-D	N-B
Flemish Cap									
F1 (204 m)	—	1.0	1.1	—	1.2	1.3	—	0.60	0.52
F2 (205 m)	—	—	0.9	—	—	0.7	—	—	0.57
Southeast Shoal									
S1 (55 m)	1.2	—	1.3	0.8	—	0.8	0.28	—	0.27
Browns Bank									
C3 (110 m) S	0.4	0.3	0.5	1.0	1.0	0.7	0.28	0.18	0.25
W	0.5	0.5	0.7	0.8	0.7	0.8	0.42	0.34	0.29
C4 (110 m) S	0.7	0.6	0.7	1.1	0.9	0.8	0.37	0.22	0.24
W	0.6	0.6	0.7	0.6	0.6	0.7	0.39	0.34	0.44
C7 (115 m) W	0.6	0.6	1.1	0.7	0.7	0.7	0.31	0.29	0.31
C8 (111 m) W	0.5	0.4	0.4	0.8	0.6	0.8	0.30	0.29	0.24
C9 (53 m) S	1.0	—	1.2	0.9	—	1.2	0.12	—	0.12
W	1.1	—	1.1	0.8	—	1.1	0.31	—	0.23
C10 (71 m) S	0.5	0.5	0.4	0.8	0.8	0.6	0.21	0.15	0.15
W	0.5	0.4	0.5	0.7	0.6	0.9	0.31	0.25	0.16
Georges Bank									
G1 (203 m)	—	0.8	—	—	0.5	—	—	0.20	—
G2 (46 m)	2.2	—	2.2	0.5	—	0.9	0.06	—	0.05
G3 (46 m)	1.8	—	1.8	0.6	—	0.6	0.06	—	0.05
G5 (75 m)	1.3	1.3	—	0.8	0.9	—	0.09	0.08	—
G6 (75 m)	1.2	1.2	—	0.6	0.9	—	0.09	0.06	—
G7 (63 m)	1.5	1.7	—	0.6	1.0	—	0.13	0.07	—

iability in the along-bank direction on the sides of Browns Bank and in the cross-bank direction on the northern side of Georges Bank. The along-bank total standard deviation is typically several times the along-bank mean current magnitude, while the cross-bank standard deviation typically exceeds the weaker cross-bank mean by an order of magnitude or more; the most notable exception to the former tendency is on the northern side of Georges Bank where the along-bank mean current is comparable in magnitude with the total standard deviation (also see Butman et al. 1982).

Comparison of the total and subtidal standard deviations (Table 2 for the current components, Table 3 for the total current) suggests that tidal and/or inertial currents make a large contribution to current variability on all four banks. As expected, the variance associated with these "high-frequency" currents dominates the temporal variability on Browns and Georges banks, while it accounts for about 90 and 70% of the total current variance on Southeast Shoal and Flemish Cap, respectively. This high-frequency variance is the main contributor to the total variance's anisotropy (Table 3) and inverse dependence on water depth on Browns and Georges banks. It is also slightly (10–20%) reduced below the near-surface region.

The subtidal standard deviations of the current components (Table 2) are generally in the range 0.02–0.06 $m \cdot s^{-1}$ on Flemish Cap, Southeast Shoal, and Georges Bank and in the range 0.05–0.15 $m \cdot s^{-1}$ on Browns Bank. The subtidal standard deviations reported by Butman et al. (1982) for (generally longer) current records from other sites on Georges Bank are larger than those for the sites discussed here, but generally less than those on Browns Bank. Finally, the subtidal standard deviation ratios (Table 3) show some suggestion of greater variability in the along-bank direction, particularly on the sides of Browns Bank in winter and on Georges Bank.

In summary, this statistical description suggests that (a) both the along-bank and cross-bank (except on Flemish Cap) current components generally have mean values which are significantly different from zero, although the along-bank mean is typically substantially larger, consistent with a clockwise gyre; (b) each component's total standard deviation greatly exceeds its mean, in general; (c) most of the current variance on all four banks is associated with tidal and inertial currents; (d) for the along-bank component, the subtidal standard deviation is comparable with the mean, while for the cross-bank component, the standard deviation generally exceeds the mean; (e) the current variability on Browns and Georges banks is several times that on Flemish Cap and Southeast Shoal, primarily due to stronger tidal currents; and (f) the subtidal current variability on Browns Bank is greater than on the other three. Since a large fraction of the current variability is associated with the tides which have known time scales, this type of statistical description may be useful to some biological–physical problems. However, for most interaction problems, a more detailed description of the current variability (e.g. of the frequency structure) and of the integrated effects of both the mean and time-varying currents is required.

It should also be noted that the "biological" significance of

current means and fluctuations may differ from their purely "statistical" significance. For example, the standard errors of the mean currents in Table 2 do not include contributions from the tidal and inertial currents and have been adjusted for the autocorrelated components of low-frequency current, although such currents may be of great significance to the short-term movement of biological organisms. Note that the low-frequency current standard deviations are generally an order of magnitude larger than the standard errors (Table 2), and the low-frequency current variance is itself only a very small fraction of the total variance (also see current spectra in Fig. 6). Indeed, a region may have a statistically significant mean current but the hourly-, daily-, or even weekly-averaged current may seldom (if ever) correspond to this mean.

Vertical Exchange

Space and Time Scales

The vertical distribution of planktonic organisms and water mass properties in the ocean is strongly influenced by the intensity and variability of the physical processes contributing to vertical exchange. These processes (e.g. Denman and Gargett 1983) involve the difficult-to-measure vertical component of velocity, either its time-mean as in upwelling-downwelling or its time-varying part as in turbulent mixing, entrainment at the boundary of a mixed layer, or internal wave displacements.

An *integral time scale* for vertical exchange may be taken as the time T_v required for vertical redistribution of a passive scalar over a specified vertical interval ΔZ. This vertical exchange time should be important to the vertical flux of inorganic nutrients across the pycnocline during the stratification season, in which case the appropriate vertical interval would be the pycnocline thickness; to the vertical redistribution of regenerated nutrients in an unstratified water column, in which case the water depth would be the relevant vertical interval; and to the vertical position (and hence ambient light intensity) of phytoplankton in the euphotic zone, in which case the surface mixed-layer or euphotic-zone depth might be the relevant interval. As a result, this physically imposed time scale should have a significant influence on photosynthetic parameters such as the phytoplankton doubling time, especially in nutrient- and/or light-limited conditions. The vertical exchange time should also be important to the vertical redistribution of neutrally buoyant eggs or immotile larvae out of, or into, a favourable feeding environment such as possibly the surface or bottom mixed layer and to other hypotheses in Bakun et al.'s (1982) first category ("vertical stability processes") of physical influences on larval survival.

Alternatively, vertical exchange may be characterized by an *integral space scale*, such as the vertical exchange distance L_v of a passive scalar in a specified time interval ΔT. The ratio of this scale to other space scales, such as the mixed-layer or euphotic-zone depth or the pycnocline thickness, may be particularly useful in the quantitative examination of hypotheses for vertical mixing influences on local food concentration or larval distributions as factors in successful feeding by newly hatched larvae (e.g. Lasker 1975; Bakun et al. 1982). In such applications, the specified time interval might be taken as Blaxter and Hempel's (1963) "point of no return," the time from when larvae are first capable of taking food to when (without food) they become too weak to feed.

In this section, we examine the magnitude and variability of space and time scales for one mechanism of vertical exchange across the pycnocline, namely for vertical diffusion by turbulent mixing, using existing parameterizations and moored measurements from the four northwestern Atlantic banks.

Method of Determination

An accurate determination of the turbulent mixing rate across the pycnocline on a submarine bank requires either repeated vertical profiles of small-scale velocity and temperature fluctuations (e.g. Denman and Gargett 1983; Oakey 1985), or ambitious (and perhaps logistically impractical for such locations) dye diffusion experiments (e.g. Kullenberg et al. 1974). Such observations are not available for the offshore banks on the northwestern Atlantic shelf, with the exception of a limited set of small-scale turbulence measurements taken recently on Georges Bank (E. P. W. Horne, J. W. Loder, and N. S. Oakey, in prep.). Here, we examine the intensity and variability of vertical mixing using available semi-empirical parameterizations to derive time series of the vertical eddy diffusivity K_v from moored measurements of horizontal velocity and density. The emphases are on the integral-scale approach and the spatial and temporal variability, and it should be noted that the parameterizations have not been verified for these particular oceanographic regimes.

We use the parameterization

$$(1)\quad K_v(t) = K_0 F(Ri)$$

where $K_0(t)$ is the diffusivity that would occur in the absence of stratification ($Ri = 0$), $Ri(t)$ is a gradient Richardson number, $F(Ri)$ is a function representing the influence of stratification, and t is time. The neutral diffusivity K_0 is taken to have the same value as the vertical eddy viscosity in steady-flow Ekman layers which are shallower than the water depth (Csanady 1976), so that it can be written

$$(2)\quad K_0(t) = \frac{C_D q^2}{200 f}$$

where $q(t)$ is the depth-averaged current for the vertical interval under consideration, C_D is a bottom drag coefficient appropriate to a depth-averaged current (taken as 2.5×10^{-3} after Greenberg 1979), and f is the local Coriolis parameter. Clearly, this formulation provides only a crude approximation, at best, to the neutral diffusivity since (i) the bottom Ekman layer generally does not extend across the entire pycnocline, (ii) the differing contributions to vertical mixing from the time-varying rotary components of velocity (e.g. Soulsby 1983) are not resolved, and (iii) turbulence arising from internal vertical shear may not be adequately represented. However, it does provide a quantitative framework in which the temporal variability and interbank differences of a primary component of turbulent mixing on at least three of the four banks (perhaps not Flemish Cap) can be examined.

The gradient Richardson number is evaluated from

$$(3)\quad Ri(t) = \frac{g \Delta\rho \Delta z}{\rho_0 |\Delta u|^2}$$

where $\Delta\rho(t)$ and $\Delta u(t)$ are the density and vector velocity differences across the vertical interval Δz, g is the gravitational acceleration, and ρ_0 is a reference density. The tendency of increased stratification to suppress turbulent mixing is commonly represented by taking F to be a decreasing function of Ri, but numerous and widely different forms have been used

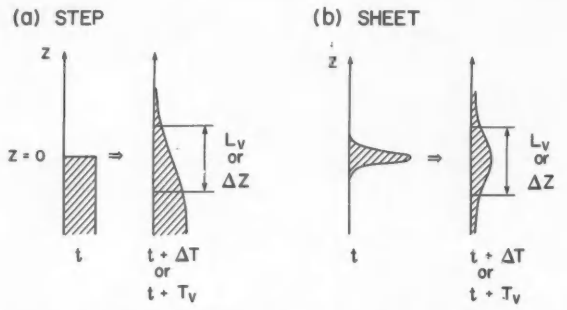

FIG. 2. Schematics showing evolution of scalar field in a medium of constant K_v and interpretations of $L_v(t,\Delta T)$ and $T_v(t,\Delta Z)$ for (a) an initial step-change in scalar concentration, and (b) an initial horizontal sheet with a Gaussian vertical distribution.

(e.g. Blumberg 1977; Henderson-Sellers 1982). In the absence of a verified form for the banks under consideration, we present results for two forms:

$$(4a)\quad F_1(t) = (1+3.3Ri)^{-3/2}$$

and

$$(4b)\quad F_2(t) = (1+0.3Ri)^{-3/2}.$$

The former was proposed by Munk and Anderson (1948) for the thermocline under wind forcing, while James (1977) obtained the latter from a model study of the seasonal evolution of a tidal front in the Celtic Sea. The extreme uncertainty in the appropriate parameterization for the influence of stratification is immediately apparent, since $F_2/F_1 = 36$ in the limit $Ri \longrightarrow \infty$.

Using (1)–(4), time series of K_0, Ri, and K_v can be obtained for locations with simultaneous moored current and density measurements at two (or more) vertical positions. Assuming that these positions are spaced closely enough to resolve the dominant horizontal velocity, vertical shear, and density gradient, the derived parameters may then be applied to the intervening vertical Δz. The determination of integral space and time scales for vertical diffusion now requires a model for the evolution of a scalar field given a time-dependent eddy diffusivity.

For guidance in the definition of the integral scales, we first consider two simple initial conditions for a vertial concentration profile in a medium of *constant* diffusivity (Fig. 2): (a) a step change in concentration which might approximate, for example, the nutrient distribution across a sharp pycnocline; and (b) a thin horizontal sheet of the diffusing material which could represent a layer of fish eggs, immotile larvae, or food particles. The subsequent evolution of the step change is described by the error function, erf η, where $\eta = z/(4K_v t)^{1/2}$ is a similarity variable and z is the vertical position measured from the location of the step, while the sheet evolves as a Gaussian, $\exp(-\eta^2)$, centered on $z = \eta = 0$ (see Csanady 1973 for more details on this approach). In either case the thickness of the diffusing layer, which we take as the integral space scale for vertical diffusion or the vertical diffusion distance L_v, may be defined as that bounded by a particular value of $|\eta| = \eta_c$ such that

$$(5)\quad L_v^2 = 16\eta_c^2 K_v t$$

where η_c has a specific interpretation in terms of each concentration profile (see below).

With *time-dependent* diffusivity, similarity solutions are generally not available for the above profiles. However, under the assumption of slowly varying diffusivity, the scalar evolution can be approximated by a succession of similarity solutions for each interval Δt for which an estimate K_v is available. Thus, in the case of time-dependent K_v, we take the vertical diffusion distance in the specified time interval ΔT as the layer thickness estimated from

$$(6a)\quad L_v^2 = 16\eta_c^2 \Delta t \sum_{t_i=t}^{t+\Delta T} K_v(t_i)$$

or

$$(6b)\quad L_v = 4\eta_c [\Delta t \sum_{t_i=t}^{t+\Delta T} K_v(t_i)]^{1/2}$$

where Δt is the constant interval of the K_v time series. Furthermore, for definiteness, we choose $\eta_c = 1/\sqrt{2}$ which corresponds in the constant diffusivity case to $L_v = 2\sqrt{3}\sigma$ (2σ) for the initial step (sheet) distribution, where σ^2 is the mean-square displacement of diffusing particles about $z = 0$. Then, the layer of thickness

$$(7)\quad L_v(t,\Delta T) = 2\,[2\Delta t \sum_{t_i=t}^{t+\Delta T} K_v(t_i)]^{1/2},$$

centered on $z = 0$, contains 68% (52%) of the diffusing particles across (from) the initial step (sheet).

Similarly, an integral time scale, $T_v(t,\Delta Z)$, for vertical diffusion over a specified interval ΔZ may be defined by the minimum value of T for which

$$(8)\quad L_v = 2\,[2\Delta t \sum_{t_i=t}^{t+\Delta T} K_v(t_i)]^{1/2} \geqslant \Delta Z$$

is satisfied (with $\Delta Z \leqslant \Delta z$ in principle). Here, L_v again corresponds to the layer thickness representing $2\sqrt{3}\sigma$ (2σ) for the initial step (sheet) distribution. Time series of both the integral space and time scales for vertical diffusion can now be calculated from the time-varying diffusivities according to (7) and (8), respectively, with each value corresponding to a specific start time for the diffusion of the initial distributions considered.

An attractive feature of this approach (if an observationally verified parameterization can be obtained) is the potential inference of the long-term variability of vertical turbulent diffusion from moored current and density measurements. Other parameterizations of K_v or some other mixing parameter in terms of easily measured quantities would be equally compatible with the formalism. One such parameterization of K_v is that inferred by Kullenberg et al. (1974) from dye diffusion experiments in the Great Lakes and applied by Cota et al. (1987) to the vertical nutrient flux in Barrow Strait, although it requires higher-frequency sampling and increased data analysis. The highest priority, however, is the field verification of these and other turbulence parameterizations, for example with detailed microstructure profiles at current meter mooring sites.

Application to Northwestern Atlantic Banks

There is one site on each of Flemish Cap, Southeast Shoal, and Browns Bank and two sites with short records on the plateau of Georges Bank from which moored measurements of current, temperature, and salinity at two or more vertical positions are available (see Table 4 for sites and vertical intervals). The vertical intervals encompass a large fraction of the summertime pycnoclines in Drinkwater and Trites' (1986, 1987) hydrographic data summaries for Browns, Georges, and the Grand Bank, while the Flemish Cap interval covers the lower third of the Drinkwater and Trites (1986) surface-to-bottom

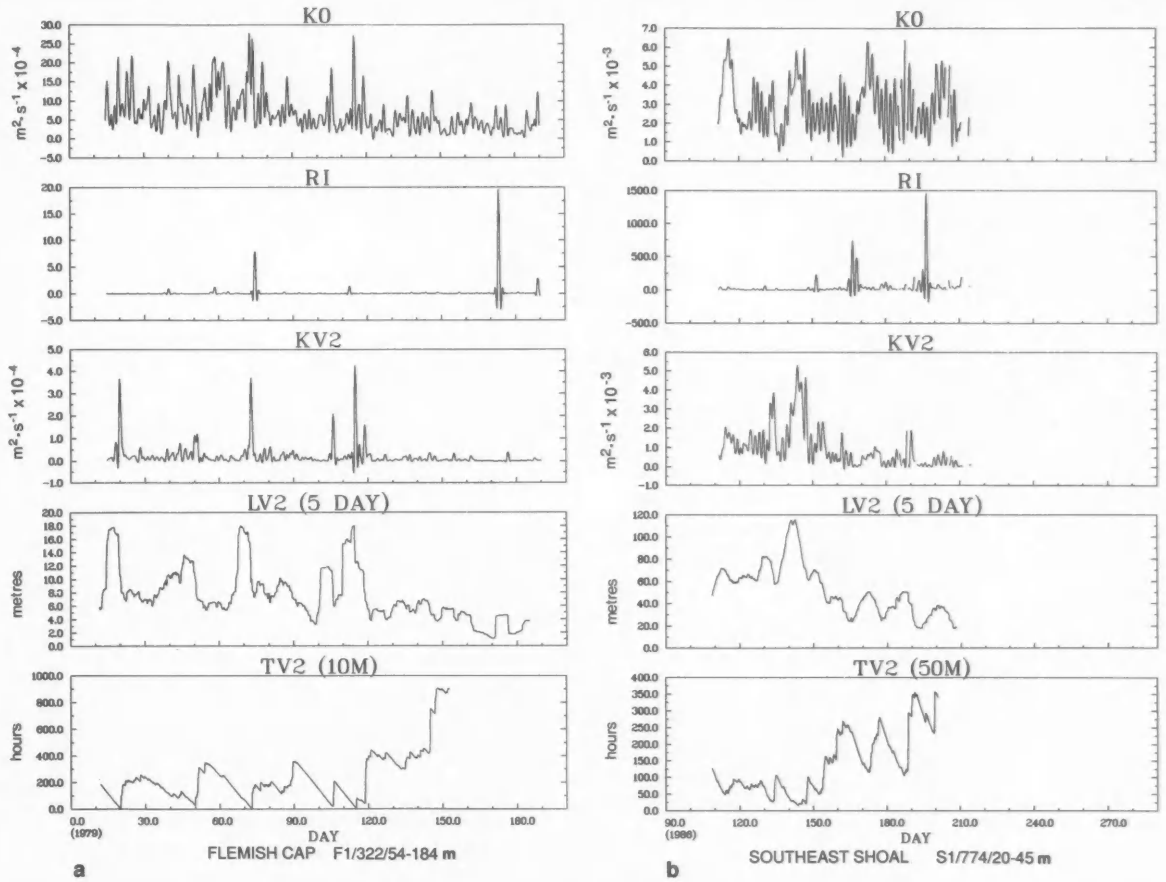

FIG. 3. Computed time series of the neutral eddy diffusivity K_0, the Richardson number Ri, the vertical eddy diffusivity K_ν, the vertical diffusion distance L_ν, and the vertical diffusion time T_ν for (a) site F1 on Flemish Cap, (b) site S1 on Southeast Shoal, (c) site C10 on Browns Bank, and (d) sites G3 and G7 on Georges Bank (see Fig. 1 and Table 2 for site locations and base of figures for instrument positions). The K_ν time series are obtained using F_2 (Ri), the values of L_ν are for the specified time interval of 5 d, and the values of T_ν are for the specified vertical interval of 10 m for Flemish Cap and 50 m for the other banks. The time series of K_0, Ri, and K_ν have been low-pass filtered (half-power period of 31 h) for display purposes. (*Fig. 3 continued next page*)

density difference. Vertical coherence and autospectral analyses on the velocity and density records at these sites indicate that, except on Flemish Cap, each of velocity and density is highly coherent across the set vertical interval in the energetic tidal/inertial and low-frequency bands, suggesting that the dominant contributions to depth-averaged current, velocity shear, and vertical density gradients are resolved. On the other hand, the Flemish Cap velocities generally have only marginal coherence in these bands, so that the K_ν estimates for Flemish Cap should be viewed with particular caution.

To illustrate the temporal variability of the mixing parameters defined in the preceding subsection, Fig. 3 presents computed time series of K_0, Ri, K_ν (using F_2), L_ν (for $\Delta T = 5$ d), and T_ν (for $\Delta Z = 10$ or 50 m) for the available records on Flemish Cap and Southeast Shoal, for the upper vertical interval during one deployment at the Browns Bank site, and for the two sites on Georges Bank — one in each of the mixed (G3) and frontal (G7) areas. Each time series is computed from the 1-h data, but the time series of K_0, Ri, and K_ν in Fig. 3 have been low-pass filtered (half-power period of 31 h) for visual display purposes.

The plots indicate that the magnitude of the vertical eddy diffusivity varies over a range of time scales and, together with the frequency structure of this variability, from bank to bank. In particular, periods of higher than average K_ν are highly intermittent on Flemish Cap (Fig. 3a) where they are primarily associated with relatively high-frequency (periods of the order of days and shorter) variability in K_0. There is also significant high-frequency variability in K_ν on Southeast Shoal (Fig. 3b), with contributions from both K_0 and Ri, but variability at the monthly modulation period of the tidal currents, contributing through K_0, is also apparent. In contrast, variability at the monthly tidal period dominates the filtered time series of K_ν for Browns Bank (Fig. 3c) and the Georges Bank mixed site (Fig. 3d), with the weaker, relatively high-frequency subtidal variability on these banks arising primarily through Ri. These

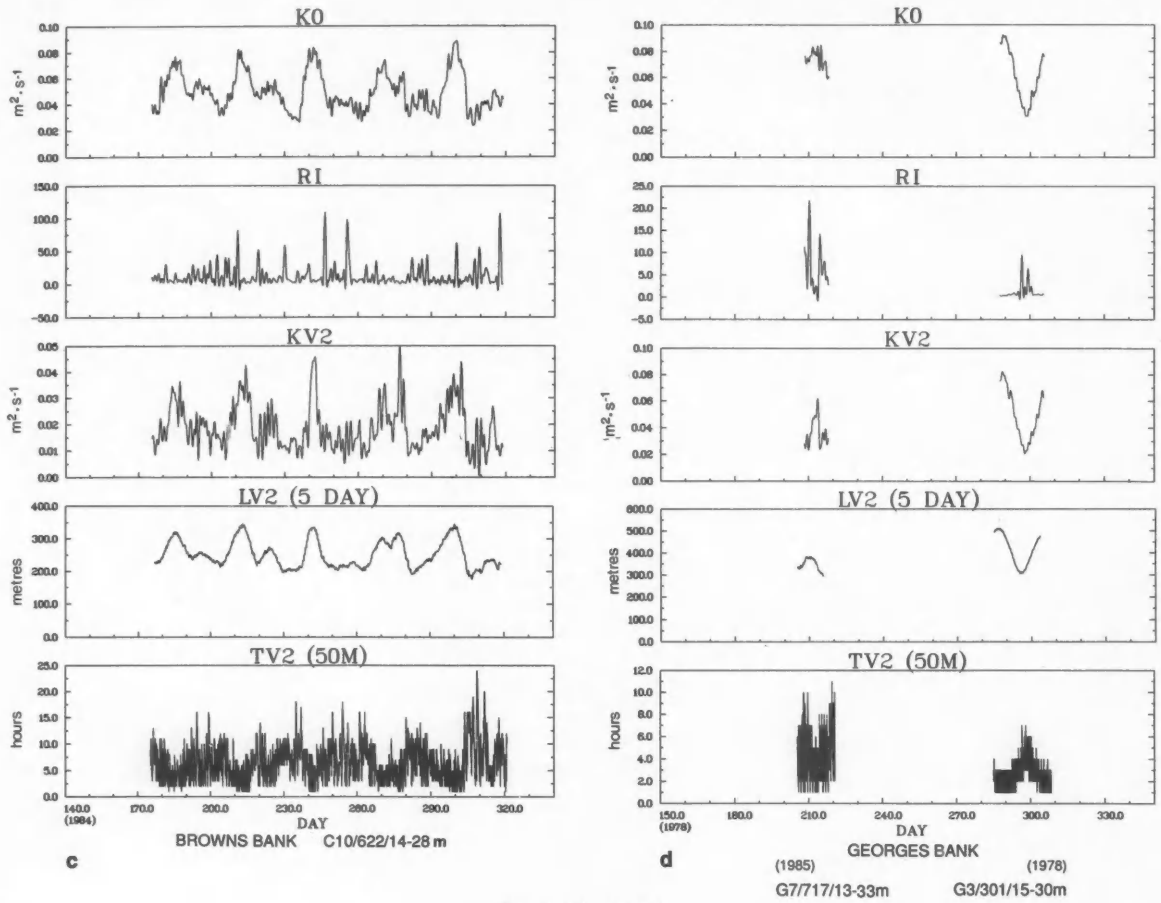

FIG. 3. (*Concluded*)

general features are also present in the K_v time series for the other deployments on Browns Bank and for the other stratification parameterization F_1 (Ri).

The temporal variability in K_v on the seasonal time scale and the spatial variability from bank to bank are illustrated more clearly in Fig. 4, which shows the monthly means of K_v computed using F_2 (Ri) for all the available records at the sites considered. The time series are too short for a statistical determination of any seasonal cycles, but a transition from wintertime high values to summertime lower values is apparent for Flemish Cap (April–May), Southeast Shoal (May–June), and Browns Bank (February–March), as well as a summertime to wintertime transition on Browns Bank in November. Similar transitions are also apparent in the time series of monthly means of K_v computed with F_1 (Ri). For "winter" and "summer" seasons tentatively defined on the basis of these monthly means, Table 4 summarizes the seasonal means of K_v for the various banks and vertical intervals and for both F_1 (Ri) and F_2 (Ri). The parameterizations under consideration and the limited observations suggest that the average value of K_v is about an order of magnitude lower in summer than in winter on Flemish Cap and Southeast Shoal and between an order of magnitude and a factor of two lower on Browns Bank in summer. The results also suggest that the average K_v value on Flemish Cap is more than an order of magnitude lower than that on Southeast Shoal, which in turn is more than an order of magnitude lower than those on Browns and Georges banks. The values on Browns Bank and in the summertime frontal zone on Georges Bank are of comparable magnitude, while those in the latter's mixed area are higher by a factor of 2 or so. It should be noted, however, that these apparent interbank differences may be partly the result of the sites and different vertical intervals for which moored measurements are available; in particular, the large vertical interval on Flemish Cap may result in an underestimation of $|\Delta y|$ and hence overestimation of Ri and underestimation of K_v, although the water depths (Table 1) and current variances (Table 2) suggest that the K_v values on Flemish Cap are likely to be substantially lower than on the other banks.

The seasonal means of K_v in Table 4 for the two different $F(Ri)$ functions also demonstrate the range of uncertainty in the actual magnitude of K_v for the existing parameterizations. Where the values of Ri are generally low (everywhere in winter, lower water column on Browns Bank and mixed area on Georges Bank in summer), the seasonal means differ by a factor of 2 or so for the two functions considered, while for intermediate Ri values (Southeast Shoal, upper water column on

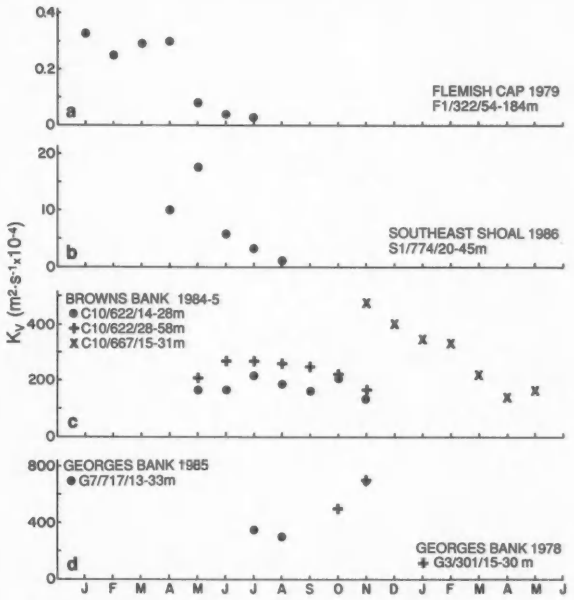

FIG. 4. Monthly mean values of K_v computed using F_2 (Ri) for (a) site F1 on Flemish Cap, (b) site S1 on Southeast Shoal, (c) site C10 on Browns Bank, and (d) sites G3 and G7 on Georges Bank.

Browns Bank, and frontal zone on Georges Bank in summer), they differ by a factor of 5–10. Furthermore, the seasonal means differ by over an order of magnitude on Flemish Cap in summer when the values of Ri are relatively large.

Although some other $F(Ri)$ functions yield K_v values outside of the ranges obtained with F_1 and F_2, the limited field observations from these banks suggest that the actual values of K_v lie within, but perhaps in the lower portion of, the ranges shown in Table 4. Loder (1985) used simple budgets for the observed changes in monthly heat content over Southeast Shoal to estimate the seasonal variation in K_v for the Shoal's pycnocline and obtained values in the ranges of (3–13) $\times$ 10^{-4} $m^2 \cdot s^{-1}$ and (0.2–0.8) $\times$ 10^{-4} $m^2 \cdot s^{-1}$ for April–May and June–August, respectively. Recently, Horne et al. (in prep.) have inferred a vertically and time-averaged (over two separate tidal periods) value of about 1×10^{-2} $m^2 \cdot s^{-1}$ for K_v from vertical profiles of turbulent dissipation in the pycnocline at site G7 on Georges Bank. These results suggest that, at least for Southeast Shoal and Browns and Georges banks (dynamically similar), the qualitative features of the interbank and seasonal variability in K_v in Table 4 are real.

The temporal variability and seasonal means of sample vertical diffusion distances and times for the northwestern Atlantic banks are also illustrated in Fig. 3 and Table 4. The vertical diffusion distances L_v are presented for the specified time interval of 5 d, which might approximate the point of no return for newly hatched larvae (e.g. Yin and Blaxter 1987). The most striking feature of the L_v time series (Fig. 3), which represent the diffusion distances of initial distributions at each time, is the reduced high-frequency variability compared with that in K_v. This occurs because the computation of the diffusion distance time series involves the low-pass filtering (actually a running-mean filter) of the K_v time series, with a half-power period approximating the specified time interval. This filtering, of course, represents the physical effect of the scalar diffusion involving integration over the time-dependent turbulent mixing during the specified interval. Thus, this is an example where a physical–biological interaction might be examined using an integral measure of the environmental conditions during a biologically determined time period, even though higher-frequency environmental variability is the main contributor to the integral parameter. An implication for larval feeding hypotheses might be that, in the case of hatching occurring in an unfavourable food environment near a food source, the probability of larval survival would be similar for all hatching that occurs within a time period equal to the point of no return preceding a physical mixing event (assuming other factors equal and the

TABLE 4. Seasonal means of K_v, L_v for the specified time interval of ΔT = 5 d, and T_v for the specified vertical interval of ΔZ = 50 m for mooring sites on the four northwestern Atlantic banks. The depth intervals encompassed by the vertical positions of the moored measurements at each site are indicated. The months considered in each season are also indicated, and results are presented for both F_1 (Ri) and F_2 (Ri). The vertical diffusion time exceeded the length of record at site F1.

	Winter							Summer						
		K_v ($m^2 \cdot s^{-1}$)		L_v (m)		T_v (h)			K_v ($m^2 \cdot s^{-1}$)		L_v (m)		T_v (h)	
Site (depth interval)	Months	F_1 ($\times 10^{-4}$)	F_2 ($\times 10^{-4}$)	F_1	F_2	F_1	F_2	Months	F_1 ($\times 10^{-4}$)	F_2 ($\times 10^{-4}$)	F_1	F_2	F_1	F_2
Flemish Cap														
F1 (54–184 m)	Jan.–Apr.	0.01	0.3	2	9	>Record length		May–July	0.002	0.05	0.7	4	>Record length	
Southeast Shoal														
S1 (20–45 m)	Apr.–May	6	10	40	70	200	70	June–Aug.	0.7	3	10	40	600	200
Browns Bank														
C10 (14–28; 15–31 m)	Nov.–Feb.	300	400	300	400	7	4	Mar.–Nov.	20	200	90	300	50	7
C10 (28–58 m)								May–Nov.	90	200	200	300	20	5
Georges Bank														
G3 (15–30 m)								Oct.–Nov.	300	600	300	400	5	2
G7 (13–33 m)								July–Aug.	60	300	200	400	20	4

probability of larval survival to be the same for all times less than the point of no return).

The seasonal means of L_v shown in Table 4 are computed from the monthly means of L_v and for the seasons inferred from the K_v values. The interbank and seasonal variability in L_v is reduced relative to that in K_v, due to L_v's dependence on the square root of K_v in the present scalar evolution model. Thus, interbank and seasonal variability in biological–physical interactions involving vertical (or horizontal) diffusion may be less than implied by variability in the magnitude of K_v (of course, the nonlinearity of many biological–physical interactions may dominate this influence). The available data and parameterizations considered here suggest that the 5-d vertical diffusion distance is generally much less than the water depth or pycnocline thickness on Flemish Cap, comparable with the same on Southeast Shoal, and much greater than the same on Browns and Georges banks.

The vertical diffusion times T_v are presented for the specified vertical interval of 50 m, except for Flemish Cap where results are shown for a 10-m interval, since the diffusion times for the 50-m interval exceed the available record length (and hence cannot be computed). The diffusion times computed from (8) correspond to the length of a running-mean filter on the K_v time series required for the integrated power under the filter to exceed a critical value determined by the specified vertical interval. It can be seen from the T_v time series in Fig. 3 that this computation removes high-frequency variability at periods shorter than the diffusion time; on Flemish Cap (Fig. 3a) and Southeast Shoal (Fig. 3b) where T_v is of order 100 h for the chosen vertical intervals, there is little variability on the time scale of days and shorter, but on Browns and Georges banks (Fig. 3c, 3d) where T_v is of order 10 h, substantial variability on this time scale remains. The implication is that, for a set vertical interval, the vertical diffusion time has more high-frequency (periods of order days or less) variability in high-energy environments where its magnitude is lower (e.g. Browns and Georges banks), suggesting for example that banks with high rates (short times) for diffusive nutrient supply across the pycnocline may have temporal variability in this supply rate over a wider range of time scales. Furthermore, in records with prolonged periods of low K_v and intermittent mixing events as on Flemish Cap (Fig. 3a), the T_v time series exhibit a sawtooth pattern with values increasing linearly as each mixing event approaches.

The seasonal means of T_v (Table 4), computed from the monthly T_v means and for the K_v seasons, show interbank and seasonal variability consistent with that already discussed for K_v and L_v. If the computed values of K_v are indeed appropriate to the 50-m interval considered, then the time scale for exchange over the entire water column is in the range of hours to days on Browns and Georges banks and days to weeks on Southeast Shoal and is months or more on Flemish Cap. The differences in the T_v results for the two different $F(Ri)$ are also reduced in comparison with those in K_v due to the dependence on the square root of K_v.

In summary, moored current and density measurements used in existing parameterizations of vertical mixing suggest large interbank and seasonal differences in the integral space and time scales for vertical diffusion on the four northwestern Atlantic banks. In general, the diffusion time scale and its seasonal change decrease markedly in proceeding from the relatively deep Flemish Cap to the shallow Southeast Shoal to the tidally energetic Browns and Georges banks. The results also point to other interbank differences in the temporal variability of the integrated effects of vertical mixing, but further field observations of small-scale turbulence and its relationship to moored current and density measurements are required before the biological implications can be addressed in detail. The implications of the present results are further discussed in the concluding section, in relation to the integral space and time scales associated with horizontal currents (next three sections).

Around-Bank Circulation

Recirculation Time Scales

The dominant feature of the mean horizontal circulation on at least three of the banks under consideration is a clockwise gyre (e.g. Table 2). To begin with, it should be emphasized that the existence of a mean Eulerian (i.e. observed at a fixed point in space) current directed along isobaths in a common sense at all around-bank positions does not necessarily imply that individual water parcels follow closed trajectories of the same sense, or even move in the same sense. The occurrence of energetic current fluctuations in the cross-bank direction at tidal and other frequencies (Table 2) can result in water parcels being completely displaced from the region of gyre-like circulation, or periodically moved to a region where the fluctuating along-bank current has a different magnitude so that a Stokes velocity (a mean water-parcel drift relative to the mean Eulerian current) arises (e.g. Longuet-Higgins 1969). In the latter case, the actual mean velocity of a water parcel (the mean Lagrangian velocity) is the sum of the mean Eulerian and Stokes velocities and may have both a different magnitude and direction than the mean Eulerian velocity (e.g. Loder and Wright 1985). In the former case, in the extreme situation of relatively rapid cross-bank exchange by the fluctuating currents, the existence of a mean Eulerian gyre may be of little significance to water parcel movement.

One way of assessing the significance of a mean gyre is to compute an *integral time scale* for around-bank recirculation under the assumption that water parcels are not displaced from the gyre and compare this recirculation time with some integral time scale for cross-bank exchange (next section). Because of the possible occurrence of a Stokes velocity, it is appropriate to consider two recirculation times: an Eulerian recirculation time defined as the time for one complete circuit of the bank as inferred from mean Eulerian current measurements and a Lagrangian recirculation time defined as the average time for one complete circuit as inferred from drifter observations. The latter, by definition, should be the more appropriate measure of recirculation, but the former is also of interest because the Stokes velocity is typically much smaller than the mean Eulerian velocity, and the Eulerian current database is generally much larger than the Lagrangian database for the banks under consideration.

Method of Determination

The Lagrangian recirculation time T_L for a particular period can be readily calculated as the mean of the recirculation times of all recirculating drifters during that period, although the reliability of this estimate is usually limited by the number of such realizations. The Eulerian recirculation time for a particular time period may be defined as

$$(9)\quad T_e \equiv \oint \frac{dy}{\bar{v}\,(y)}$$

where $\bar{v}$ is the around-bank mean current during that period and the integration is over a closed circuit around the bank. The limitation in this case is that Eulerian current measurements are typically available from only a few positions, and an assumption must be made regarding the currents at other around-bank locations. The crudest assumption, of course, is that a single measurement is representative of all around-bank locations in which case (9) yields $T_e = C/\bar{v}$ where C is the length of the closed circuit.

A potential improvement on this crude estimate can be obtained with some assumptions about the dynamics of the circulation and quantitative information on the bank's bathymetry. One such assumption is that, to lowest order, the around-bank mean flow satisfies conservation of potential vorticity in which case it is along geostrophic (f/h where f is the Coriolis parameter and h is the water depth) contours (e.g. Moore 1970). Then, with the assumptions that f is uniform over a particular bank and that volume conservation is satisfied, the flow follows depth contours with magnitude (e.g. Janowitz and Pietrafesa 1982)

$$(10)\quad \bar{v}(y) = \frac{\bar{v}}{dh/dx}\Big|_{y=0} \frac{dh}{dx}(y)$$

where (x,y) are now the local (cross-bank, along-bank) coordinates. Thus, the mean current at all around-bank positions on a particular isobath can be determined from measurements at a single site ($y = 0$) on this isobath and bathymetric information. The Eulerian recirculation time for this isobath is then

$$(11a)\quad T_e = \frac{dh/dx}{\bar{v}}\Big|_{y=0} \oint \frac{dy}{dh/dx}$$

which can be evaluated from

$$(11b)\quad T_e = \frac{dh/dx}{\bar{v}}\Big|_{y=0} \sum_{i=1}^{n} \frac{\Delta y_i}{(dh/dx)_i}$$

where Δy_i and $(dh/dx)_i$ are the length of the isobath and the average bottom slope in various around-bank sectors in which the slope can be approximated as uniform. This approach can also be used to infer Lagrangian recirculation times for drifters which do not complete a circuit of the bank, in which case T_e and $\bar{v}$ in (9)–(11) are replaced by T_L and the mean Lagrangian velocity $\bar{v}_L$.

A further modification of this approach could be the use of numerical model predictions of $\bar{v}(y)$ (e.g. Greenberg 1983; Greenberg and Petrie 1988), either in conjunction with Eulerian or Lagrangian current measurements, or computing T_e as an integral diagnostic parameter of the predicted circulation.

Application to Northwestern Atlantic Banks

The estimated recirculation times for the four northwestern Atlantic banks are summarized in Table 5. Except for the Georges Bank estimates, the Eulerian times are based on the moored measurements summarized in Table 2 and the Lagrangian times on the available trajectories of satellite-tracked drifting buoys drogued at 2–10 m. The latter include trajectories for the Newfoundland Shelf provided by the International Ice Patrol and oil companies (B. D. Petrie, Bedford Institute of Oceanography, pers. comm.), as well as those obtained during the experiments noted earlier. Two sample trajectories for each of Flemish Cap, Southeast Shoal, and Browns Bank are shown in Fig. 5.

The Eulerian recirculation time for the subsurface waters on the 200-m isobath on Flemish Cap, based on the longest current records (at 54 and 184 m below the surface at site F1 for January–July) and obtained from (11b) with $n = 6$ (Fig. 5a), is 120 d. However, this estimate varies with the averaging period of $\bar{v}$: for January–April, the time is reduced to 75 d and for March (when the limited observations suggest the most intense gyre) to 48 d. These estimates are about 25% lower than those obtained assuming uniform bathymetry around the Cap and, for January–April, are comparable with those inferred from the moored measurements at site F2.

The near-surface Lagrangian recirculation time has been estimated for the 200- and 400-m isobaths on Flemish Cap, using the Lagrangian form of (11b) with $n = 6$ and 8, respectively (Fig. 5a). Of the 20 drifter tracks available for the Flemish Cap region, 18 show some support for a clockwise gyre but there is only one complete circuit of the Cap. On the basis of this circuit (in only 16 d in June of a different year from the Eulerian measurements) and four partial circuits, a Lagrangian recirculation time of 36 d is obtained for the 200-m isobath. On the other hand, a time of 78 d is obtained for the 400-m isobath using 10 partial circuits. These results are not substantially altered with the assumption of around-bank uniformity (Table 5), and no significant seasonality is apparent. Clearly, the Flemish Cap database is inadequate for a statistically reliable determination of the magnitudes of, temporal variability in, and differences between the Eulerian and Lagrangian recirculation times, but it suggests that they are of the order of 50–100 d with substantial temporal variability. Indeed, the sample trajectories in Fig. 5a indicate an intermittent gyre.

There are no Eulerian current measurements on Southeast Shoal suitably located for the estimation of a recirculation time. Of the six available drifter tracks (all in the March–July period), only two (not shown) show some support for a gyre centered over the Shoal. Assuming the circulation to be uniform around the Shoal, the composite of these tracks suggests a Lagrangian recirculation time of 56 d (around the southern two thirds of the Shoal). A third trajectory (Fig. 5b) indicates a larger-scale clockwise gyre displaced to the west over the southern Grand Bank, similar to that in Kudlo et al.'s (1980) dynamic height field. Nevertheless, the existence of a persistent clockwise circulation over the Southeast Shoal remains uncertain.

The Eulerian recirculation time has been estimated for two isobaths on Browns Bank: the 70-m isobath surrounding its western cap from the current measurements at site C10 and the 110-m isobath from measurements at sites C3, C4, C7, and C8. Using (11b) with $n = 6$ (Fig. 5c), the recirculation time on the 70-m isobath is predicted to range from 6 d for the near-surface waters to 12 d for the near-bottom waters, with these estimates being about 40% lower than those obtained assuming uniformity around the Bank (Table 5). The estimates for the 110-m isobath are obtained using $n = 13$ (Fig. 5c) for the area extending as far east as the point where the connecting neck between Browns and Baccaro banks is narrowest (near 65°W), with the cross-neck transect not included. If the assumptions leading to (11b) are valid, then $\bar{v}\,(dh/dx)^{-1}$ should be approximately constant at the four measurement sites on the 110-m isobath; however, for the depth-averaged mean currents computed from Table 2 the observed values of this quantity range from about 6 $m \cdot s^{-1}$ at C3 and C7 on the Bank's northern side to 12 and 28 $m \cdot s^{-1}$ at C4 and C8, respectively, on the southwestern side. One interpretation of this is that there is a portion of the clockwise circulation on the southwestern side, probably associated

TABLE 5. Summary of the estimated Eulerian and Lagrangian recirculation times, and the residence times obtained using three different approaches, for specified areas (inside the given isobath) and vertical zones on the four northwestern Atlantic banks. The Flagg et al. (1982) region for Georges Bank extends 50–100 km beyond its plateau. The areas enclosed by the specified isobaths in other cases are given in Table 1. Where two estimates of the Eulerian or Lagrangian recirculation time are given, the first is obtained using the assumption of uniformity around the bank and the second using (11b) or (12). With the exception of the budget estimates of (summertime) residence time for Southeast Shoal and Georges Bank, all recirculation and residence time estimates are based on (or considered appropriate to) annual-mean conditions. See footnotes and text for further explanation.

	Recirculation times (d)		"Residence" times (d)		
	Eulerian[a]	Lagrangian[b]	Drifters[b]	Budgets	"Tidal prism"
Flemish Cap					
$h = 200$ m					
Depth-averaged	160/120 (Jan.–July) 64/48 (Mar.)				>24
Near-surface		38 ± 19 (5)/36 ± 17 (5)			
$h = 400$ m					
Depth-averaged			32 ± 17 (17)	40	
Near-surface		67 ± 20 (10)/78 ± 50 (10)			
Southeast Shoal					
Depth-averaged					>17
Near-surface		56	>28 ± 10 (5)		
Near-bottom				>100	
Browns Bank					
$h = 70$ m					
Depth-averaged					>2
Near-surface	10/6	8 ± 5 (6)/7 ± 4 (6)	9 ± 5 (19) 10 ± 4 (May–Oct.) (16) 4 ± 1 (Nov.–Apr.) (3)		
Middepth	13/8				
Near-bottom	19/12				
$h = 110$ m					
Near-surface	>40/>180	25 ± 12 (7)/63 ± 44 (7)	12 ± 9 (23) 14 ± 9 (May–Oct.) (18) 5 ± 4 (Nov.–Apr.) (7)		
Middepth	>29/>120				
Near-bottom	>62/>280				
Georges Bank					
$h = 60$ m					
Depth-averaged				20–50	>2
Near-surface			27 ± 21		
Flagg et al. 1982					
Near-surface	56 (39–77)	44 ± 11 (5)	54 ± 26 (19) 45 ± 8 (Dec.–Apr.) (10) 66 ± 28 (June–Nov.) (9)		
Middepth	82 (49–108)				
Near-bottom	104 (49–159)				

[a]Range of values in parentheses.
[b]Mean ± standard deviation computed over total number (value in parentheses) of buoy tracks.

with inflow to the Gulf of Maine (e.g. Ramp et al. 1985), which does not recirculate around the northern side of the Bank, hence accounting for the lower values of $\bar{v}\,(dh/dx)^{-1}$ there. The high value of $\bar{v}\,(dh/dx)^{-1}$ at C8 may indicate that the flow speed there is influenced by the enhanced bottom slope just upstream. Under the assumptions that volume and potential vorticity conservation hold on, but not between, the northern and southwestern/southeastern sides of Browns Bank, the Eulerian recirculation time can alternatively be estimated from

$$(12)\quad T_e = \frac{dh/dx}{\bar{v}}\Big|_{y=y_1} \sum_{i=1}^{l} \frac{\Delta y_i}{(dh/dx)_i} + \frac{dh/dx}{\bar{v}}\Big|_{y=y_2} \sum_{i=1}^{m} \frac{\Delta y_i}{(dh/dx)_i}$$

where the first summation is for the northern side ($l = 5$) and the second for the southwestern/southeastern side ($m = 8$). Taking the average $\bar{v}\,(dh/dx)^{-1}$ value from C3 and C7 as representative of the northern side and that from C4 as representative of the southwestern/southeastern side, recirculation times of 180, 120, and 280 d are obtained for the near-surface, middepth, and near-bottom waters, respectively. These could be viewed as minimum estimates, since the transit time across the eastern neck is not included, although they may also be

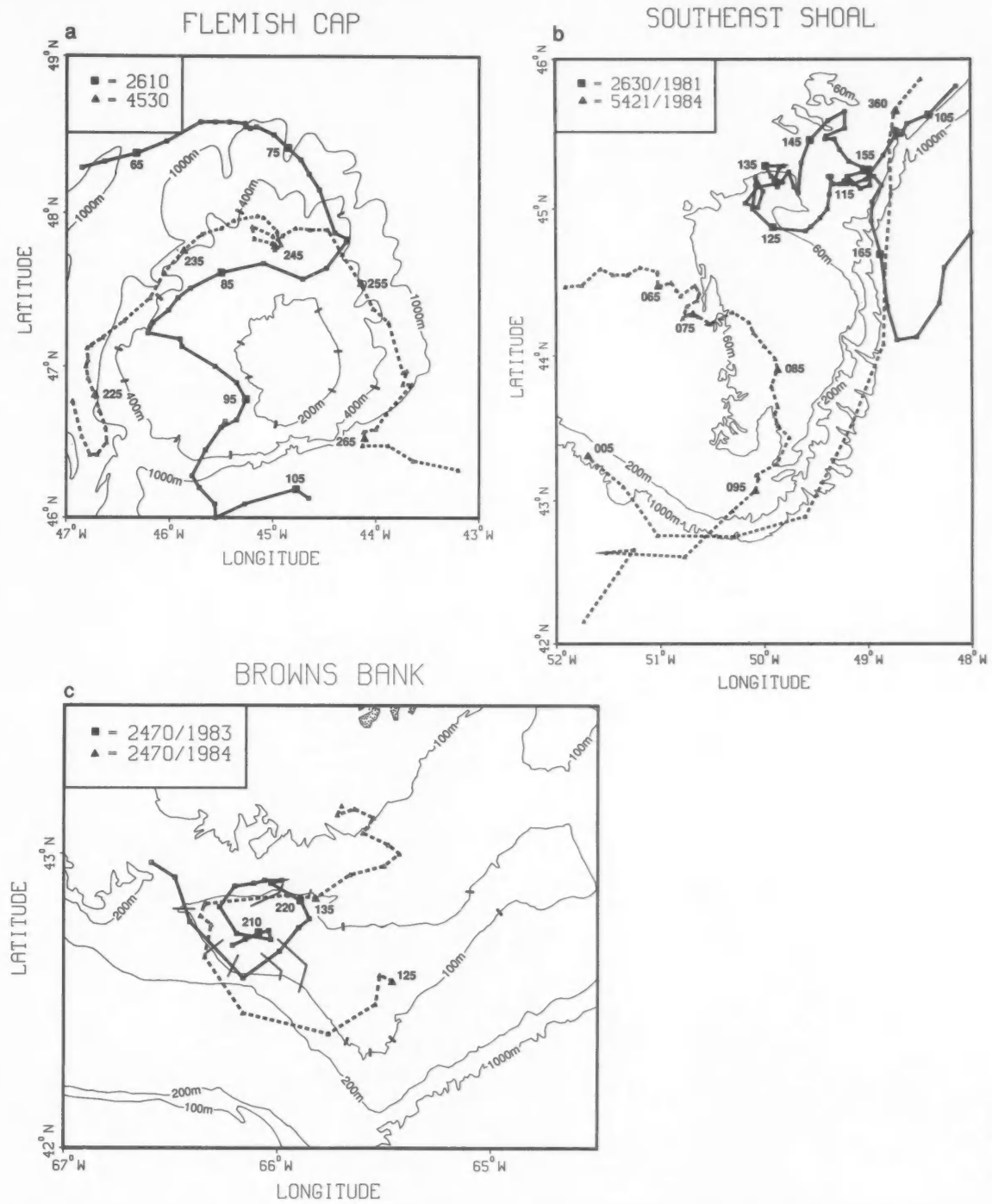

FIG. 5. Two sample drifter trajectories for each of (a) Flemish Cap, (b) Southeast Shoal, and (c) Browns Bank. For both Flemish Cap and Southeast Shoal, one trajectory shows some support for a gyre (displaced to the west on Southeast Shoal) and the other no support. For Browns Bank, one trajectory shows recirculation, while the other exits to the north, typical of many others (Smith 1988). Also indicated in Fig. 5a and 5c are the sectors on Flemish Cap and Browns Bank in which uniform bathymetry is assumed in the application of (11b).

exaggerated due to (12)'s implicit prediction of weak mean currents on the gently sloped eastern portion of the Bank. The recirculation time estimates are much shorter when it is assumed that the mean currents at sites C3/C7 and C4 are representative of the entire northern and southwestern/southeastern sides, respectively (Table 5).

Nineteen of the 32 drifter trajectories available for Browns Bank show some support for a clockwise gyre, while four of these include a complete circuit of the western cap and a circuit of the entire Bank. On the basis of the complete circuits, two partial circuits near the 70-m isobath (using (11b) with $n = 6$), and six partial circuits near the 110-m isobath (using (11b) with $n = 13$), the estimated Lagrangian recirculation times are 7 and 63 d for the 70-m (western cap) and 110-m (entire bank) isobaths, respectively. As in the Eulerian case, however, the 110-m estimate is substantially reduced if the assumption of around-bank uniformity is made (Table 5). Clearly, the recirculation time on Browns Bank is sensitive to the choice of isobath (i.e. the portion of the Bank considered) and the uncertain current strength on its eastern end.

For recirculation time estimates for Georges Bank, we use the results reported by Flagg et al. (1982) for the New England Outer Continental Shelf Physical Oceanography Program. They estimated the Eulerian recirculation time by dividing the Bank into four sectors and taking moored current measurements at four sites as representative of the sectors, with three sites being on the 85-m isobath and one on the 60-m isobath. Using the yearly-mean currents, they obtained 56, 82, and 104 d for the near-surface, middepth, and near-bottom waters, respectively, with the ranges indicated in Table 5. The Eulerian recirculation times for the seasonal-mean currents were not estimated, but the moored observations generally indicate that the clockwise flow approximately doubles in intensity between winter and late summer, implying a factor of 2 reduction in recirculation time.

Flagg et al. (1982) also examined the trajectories of 20 satellite-tracked drogued buoys for evidence of recirculation on Georges Bank. Five of these, all deployed in June–August, completed a circuit of the Bank in an average time of 44 d. This estimate of the Lagrangian recirculation time is consistent with the Eulerian recirculation time estimate for the near-surface waters, considering the expected seasonality in the latter and the prediction of a Stokes velocity (Loder and Wright 1985) resulting in the Lagrangian recirculation time being slightly greater than the Eulerian time.

Cross-Bank Exchange

"Residence" Time Scales

The significance of any around-bank mean gyre to biological processes on a bank clearly depends on the length of time that particular water parcels or organisms stay in the region of gyre-like circulation or over the bank. In general terms, a quantitative measure of this significance is the ratio of the independent integral time scales for horizontal transfer in two orthogonal directions: the recirculation time discussed in the last section for the around-bank direction and some "residence" time for exchange across the gyre or bank. However, there are difficulties in both the definition and determination of the latter.

Taking guidance from the simpler but analogous problem of estimating "residence", "flushing", or "detention" times for enclosed and semi-enclosed systems such as lakes, reservoirs, and estuaries, two different fundamental exchange times can be defined for a given spatial domain. The first, typically defined as the domain's volume divided by an appropriate measure of the cross-boundary flow rate, depends only on the physical processes occurring at those domain boundaries where exchange is taking place and hence is a measure of exchange *between* the domain and ambient regions. The flushing times estimated for estuaries using the fraction-of-freshwater and tidal prism methods (e.g. Dyer 1973) are examples. The second, usually taken to be of order L^2/K where L is the domain's horizontal scale and K is a horizontal dispersion coefficient (e.g. Fischer et al. 1979), depends on the processes occurring within the domain and hence might be more appropriately referred to as a "redistribution" time *within* the domain. The important point for the present discussion is that the residence time of some scalar in a mean gyre or over a bank may depend on both of these exchange times and may require a specific definition appropriate to the particular application. For example, when the redistribution time for a domain is of order or greater than its flushing time as defined above (i.e. relatively slow internal redistribution), the actual residence time will also depend on the location (e.g. proximity to open boundaries) of the initial distribution of the scalar (e.g. Loder et al. 1982). In the estuarine context, the modified tidal prism method for estimating flushing time (e.g. Dyer 1973) includes effects of processes both within and at the boundaries of the estuary.

Further complications in the use of a residence time arise in particular fisheries problems, such as in larval dispersion where persistence in the specified domain of only a small fraction of the initial total may be adequate for a successful year-class and where the organisms may be motile enough to use spatial structure in a temporally varying flow field to counteract mean advection and dispersion (e.g. Fortier and Leggett 1983).

Methods of Determination

From the fisheries application perspective, the ideal approach to the determination of a passive-scalar residence time for a specific domain would appear to be the release of a scalar tracer in various parts of the domain and observation of the time at which only a specified fraction of the total quantity released remains in the domain. There are of course severe logistical difficulties with such an approach in the case of large submarine banks, so that a variety of other approaches are commonly substituted.

The computation of a residence time is perhaps most straightforward when the trajectories of Lagrangian drifters such as drogued buoys are available. The residence time can then be taken as the average time that drifters released in a specified area stay in that, or some other specified area; alternatively, it can be taken as the time at which only some nonzero fraction of the drifters remain in the area. This residence-time estimate may, however, only be appropriate to the vertical level at which the drifters are drogued, typically the near-surface region, and may be misleading because the buoys are drogued to specific vertical levels rather than (vertically moving) water parcels.

A more appropriate but generally less tractable method for the determination of residence time is from budgets for conservative water mass properties in a region (e.g. Loder et al. 1982). One advantage of this approach is that, since the property concentration depends on the time integral of the scalar fluxes, the inferred exchange rates and residence times should be more statistically reliable. Furthermore, it is not necessary to resolve the temporal variability of the exchange processes.

On the other hand, assumptions regarding the spatial structure of the scalar fluxes and exchange rates must often be made in order to make the approach mathematically tractable. In the simplest case of a single reservoir with the horizontal scalar flux assumed equal to a uniform exchange rate k_0 times the scalar gradient (e.g. Klein and Steele 1985; Akenhead 1986), an exponential decay in any initial scalar gradient is expected and the decay time scale k_0^{-1} is usually taken as the residence time.

An alternative point of departure in the determination of residence time is detailed measurement of the currents and scalar fluxes together with knowledge of the contributing processes at key positions in the domain, following the conventional estuarine approach to flushing time discussed above. One obvious example of this approach is the use of eddy flux measurements (e.g. Smith 1978; Marsden 1986; Horne et al. 1988) of conservative scalars on the boundary of the domain in conjunction with scalar concentrations in the domain to infer a residence time. Another instructive, but less conclusive, example is an extension of the tidal prism method for estuaries to submarine banks whose horizontal current variance is primarily at a single frequency ω (perhaps the tidal frequency). If the standard deviation of current variability at this frequency is denoted by σ_ω, then the standard deviation of the associated horizontal water parcel excursions is simply σ_ω/ω. Now, if a measurement of σ_ω at one position on the boundary of an approximately circular bank region of radius R is assumed representative of other positions on the boundary, the standard deviation of the volume of water displaced from the fixed region by the current fluctuations is simply $(\sigma_\omega/\omega)\,2\pi Rh$ where h is the water depth on the boundary. A first estimate of a "flushing" time for the bank might then be

$$(13)\quad T_f = \frac{V}{(\sigma_\omega/\omega)2\pi Rh} \times \frac{2\pi}{\omega} = \frac{V}{\sigma_\omega Rh}$$

where V is the volume of water in the region under consideration. It must be emphasized that this estimate should be interpreted as a lower bound for the actual residence time under the assumption that current variability at frequency ω is involved in the dominant exchange process. The actual residence time will of course be substantially longer and dependent on the amount of mixing of the displaced water parcels with the ambient water during the off-bank excursions. If this mixing were independent of the current frequency (unlikely to be the case), then the total standard deviation of cross-bank current variability (σ_1 in Table 2) could be substituted for σ_ω in (13) and the resulting expression multiplied by a mixing factor to obtain a residence-time estimate. However, rather than providing reliable absolute estimates of residence time, (13) is most useful in the intercomparison of banks such as the northwestern Atlantic banks in the next subsection. The significance of cross-bank current variability and the associated water parcel excursions is discussed further in the next section.

Application to Northwestern Atlantic Banks

The available estimates of residence time for the northwestern Atlantic banks, obtained using three different approaches, are summarized in Table 5. The drifter estimates for Flemish Cap, Southeast Shoal, and Browns Bank are obtained from the satellite-tracked buoy trajectories discussed in the last section, with the residence time defined as the average time that drifters released or passing inside a specified isobath (Table 5) are within a certain distance from that isobath (15–30 km depending on the scale of the local bathymetry and/or current shear; e.g. see Smith 1988). The "drifter" estimates for Georges Bank, taken from Flagg et al. (1982), are for a wider region extending 50–100 km beyond the Bank's plateau. The sources of the limited "budget" estimates are cited below, while the lower-bound "tidal prism" estimates are obtained using the "tidal" standard deviations of current variability from Table 2 (taken as σ_1–σ_6) in (13). Note that, as discussed earlier (e.g. Table 3), the tidal and other current fluctuations in the 2- to 30-h period range account for over 60% of the total current variance on all four banks.

For the region enclosed by the 400-m isobath on Flemish Cap, the 17 relevant drifter tracks indicate a residence time of 32 d for the near-surface waters. This is comparable with the estimate of $k_0^{-1} = 40$ d for the upper 100 m, obtained by Akenhead (1986) from a salinity budget. Considering that the lower-bound tidal prism estimate in Table 5 is for the 200-m isobath (should be much longer for the 400-m isobath), it would appear that some non-tidal process is primarily responsible for cross-bank exchange on Flemish Cap. This is not surprising considering that the subtidal current variance is nearly 40% of the total variance (Table 2) and is consistent with Akenhead's (1986) conclusion that the exchange is associated with a mean inflow of Labrador Current water. The available data thus suggest that the average residence time of upper-layer water on Flemish Cap is less than the average recirculation time of the clockwise gyre, consistent with the single complete circuit by the Lagrangian drifters and suggesting a limited significance for the gyre.

The five drifters that passed inside the 60-m isobath on Southeast Shoal indicate a residence time of at least 28 d for the near-surface waters. This is in contrast with the lower layer over the Shoal in summer, for which Loder (1985) inferred a residence time of over 100 d from a heat budget. The tidal prism estimate for the Shoal is consistent with the lower layer having a residence time of this order of magnitude. The sparse data thus suggest that the residence time of upper-layer water over Southeast Shoal is less than the recirculation time of any gyre, so that the unresolved question of the existence of a gyre over the Shoal may not be of much significance to biological/fisheries processes in the near-surface region. This may be different for the lower layer however, since its residence time appears to be much longer, in summer at least.

The drifter data from Browns Bank indicate average residence times of 9 and 12 d for the near-surface waters on the western cap ($h = 70$ m) and entire Bank ($h = 110$ m), respectively, with shorter residence times in winter and early spring. The western cap estimates are comparable with the Eulerian and Lagrangian recirculation times for the near-surface waters on the 70-m isobath, while the entire-Bank estimates are substantially less than the recirculation times for the 100-m isobath. These results are, of course, consistent with the observed higher occurrence of drifter recirculation around the western cap than the entire Bank. The tidal prism estimate of residence time for the western cap is much lower than for Flemish Cap and Southeast Shoal and suggests that tidal processes may contribute significantly to cross-bank exchange.

The drifter data from Georges Bank indicate a residence time

of 54 d for the near-surface waters in the general vicinity of the Bank, with a seasonal variation (Flagg et al. 1982). These data also suggest a residence time for the central Bank (inside h = 60 m) which is in reasonable agreement with the estimate obtained by Loder et al. (1982) from a summertime heat budget. The tidal prism estimate for the central Bank is comparable with that for Browns Bank and suggestive that tidal processes play a role in cross-bank exchange here, too. Unlike the other three banks, however, the annual-mean residence time of upper-layer water on Georges Bank is comparable with the mean recirculation time of the gyre. Even if Flagg et al.'s (1982) residence times are overestimated because of the large off-bank region considered, there is a suggestion that, in summer at least, the average upper-layer residence time on Georges Bank exceeds the recirculation time. This conclusion is consistent with the relatively high number of complete drifter circuits observed on the Bank in summer and suggests that the gyre there is more likely to be significant to biological and fisheries processes than the gyres on the other three banks considered.

Horizontal Current Fluctuations

Along-Bank and Cross-Bank Excursions

In this section, we present an example of *integral space scales* for the horizontal circulation, namely for current fluctuations during a specified time interval.

The Eulerian current statistics in Table 2 summarize the magnitude of current fluctuations on the four northwestern Atlantic banks. A first partitioning of the current variance between tidal/inertial and subtidal motions is also presented, but further information on the frequency dependence of the motions is not available from such a summary. The frequency structure of the current fluctuations may be of substantial importance, however, both in determining their contributions to circulation on a particular time scale and to horizontal exchange and in determining their significance to biological processes on the banks.

One example of the importance of the current fluctuations' frequency structure is the inverse dependence on frequency of the horizontal water parcel excursion ($\pm\sigma_u/\omega$) associated with an oscillatory current variation, as used in the "tidal prism" estimates of residence time in the last section. Thus, for current fluctuations of the same amplitude, the lower-frequency fluctuations are most effective in displacing water parcels and their organisms to different physical, chemical, and biological environments where modified mixing and biological–physical interactions may occur. A quantitative measure of the significance of such displacements for cross-bank current fluctuations at a particular frequency might be the ratio of the associated root-mean-square excursion σ_u/ω to the horizontal scale of the bank, to the horizontal separation distance from an adjacent bank or other feature, or to the cross-bank scale of any gyre. The contributions of cross-bank current fluctuations at all frequencies can be included through computation of the total excursion variance over all frequencies and comparison of the square root of this variance — the total excursion standard deviation for cross-bank current fluctuations — with the banks' scales and separation distances. Similarly, a bank may also be characterized through comparison of its total excursion standard deviation for along-bank current fluctuations to an along-bank distance scale such as its circumference.

Alternatively, if current fluctuations in only a limited frequency range are of relevance to the biological or physical processes under consideration, then the excursion standard deviation for fluctuations in that frequency range alone can be used.

Finally, to assess the relative importance of the fluctuating and mean currents to water parcel displacement, these integral space scales for current fluctuations can be compared with the net displacement associated with the mean current during some specified time period.

Method of Determination

The natural first step in the determination of excursion standard deviations is the computation of the autospectrum for each current time series under consideration. The spectrum reveals the detailed frequency structure of the current variability and can be used to determine the magnitude of the current fluctuations in particular frequency bands of biological or other relevance. If $\phi_u(f_i')$ is the current spectral density in a frequency band of width $\Delta f_i'$ centered on frequency f_i', then the excursion spectral density in that same band is

$$(14)\quad \phi_e(f_i') = \frac{\phi_u}{\omega_i^2} = \frac{\phi_u}{(2\pi f_i')^2}$$

where ω_i is the corresponding angular frequency. The result is an "excursion spectrum" for each current component which can be used to determine the water parcel excursions associated with current fluctuations in the various frequency bands set by the sampling interval and length of record. The excursion standard deviation for a particular frequency range encompassed by n spectral bands is then simply

$$(15)\quad L_e \equiv \left\{ \sum_{i=1}^{n} \frac{\phi_u}{(2\pi f_i')^2}\, \Delta f_i' \right\}^{1/2}$$

which may be interpreted as the amplitude of the average water parcel excursion associated with current fluctuations in the specified frequency range. This range may be chosen to obtain either the total excursion standard deviation or the peak excursion standard deviation corresponding to the frequency at which the largest excursions occur. Note that the horizontal range of water parcel movement is twice the excursion standard deviation and that the above interpretation assumes that the current amplitude is uniform over the horizontal excursion distance.

Application to Northwestern Atlantic Banks

The total and peak excursion standard deviations computed for mooring sites on the four banks under consideration are summarized in Table 6. These are derived from the autospectra of the 1-h current time series using a common block size of 512 points, so that current fluctuations with periods in the range of 2 h to about 21 d are represented. For comparison, Table 6 also shows the mean-current displacements in 5.3 d (corresponding to one quarter of the period of the lowest-frequency current fluctuations included in the excursion estimates), computed assuming the currents to be spatially uniform over the displacement distances. The cross-bank displacements are generally much less than the respective bank's effective radius, except for Browns Bank where in some instances they are comparable with the western cap's radius, while the along-bank displace-

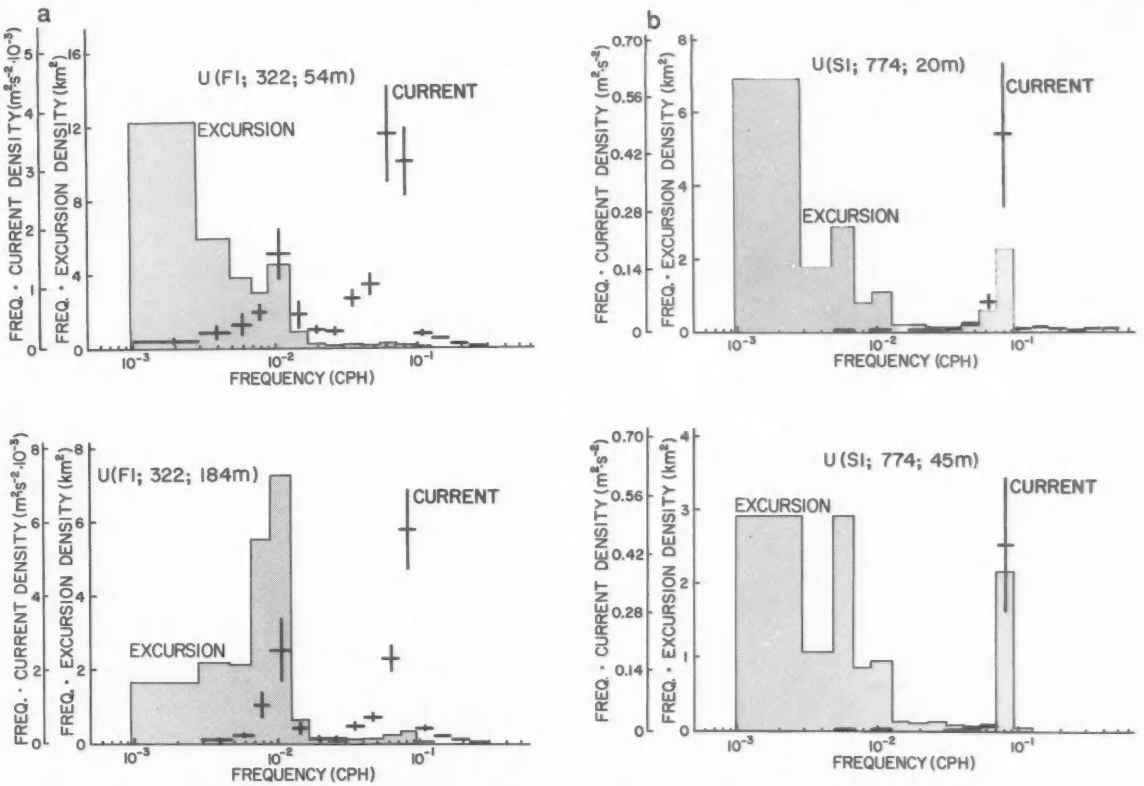

FIG. 6. Autospectra of cross-bank current and cross-bank excursion at two vertical positions at a site on each of (a) Flemish Cap, (b) Southeast Shoal, (c) Browns Bank, and (d) Georges Bank. The plots are in variance-conserving form so that the area under each spectrum is distributed in proportion to the actual energy. The confidence intervals on the current spectral estimates indicate the standard error of the mean computed through block-averaging. Corresponding standard error estimates can be calculated for the excursion spectrum. (*Fig. 6 continued next page*)

ments have an interbank variation consistent with that of the mean (Table 2) and the recirculation times (Table 5) discussed earlier.

The autospectra of cross-bank current and the associated excursion spectra are shown in variance-conserving form in Fig. 6 for two vertical positions at a mooring site on each of the banks. In general, the largest contribution to the current variance in both the along-bank (not shown) and cross-bank directions comes from the semidiurnal tidal band, consistent with Table 2, while the largest contribution to the excursion variance in both directions comes from the lowest-frequency band. The latter suggests that the total and peak excursion standard deviations might increase with a larger block size, since the variance removed in the detrending of the present blocks could contribute in the added (low) frequency bands of such red spectra. Nevertheless, the present results are useful for a first interbank comparison of the water parcel excursions associated with current fluctuations in a common frequency range and for a first assessment of the excursions' importance relative to the mean-current displacements.

At the Flemish Cap site, the total excursion standard deviations (Table 6) are of comparable magnitude for the along-bank and cross-bank directions. The along-bank excursions are about one half of the along-bank mean-current displacements, while the cross-bank excursions are substantially larger than the cross-bank mean-current displacements (at site F1 at least) but much less than the horizontal scale of the Cap (Table 1) and its separation distance from the nearest other bank, the Grand Bank (Fig. 1a). The total excursions are 30–60% larger at the upper (54 m) vertical position, primarily due to increased energy in the two lowest frequency bands. On the other hand, the lower vertical position on Flemish Cap is unusual in that the peak cross-bank excursion is associated with currents in the 93-h period band (Fig. 6a), rather than the lowest-frequency bands as in most cases. The current autospectra indicate that this wave motion (dynamics unknown) is bottom-intensified with largest amplitude ($\sim$0.03 m·s^{-1}) in the cross-bank direction.

The excursion standard deviations at the Southeast Shoal site are in the same general range as those on Flemish Cap. The along-bank excursions and mean-current displacements are of the same order of magnitude, while the cross-bank excursions are much smaller than the mean-current displacements, as well as the Shoal's effective radius. The near-surface excursions are again enhanced due to higher energy in the lowest-frequency bands (Fig. 6b), particularly in the along-bank (north–south) direction.

The Browns Bank excursion standard deviations are generally 2–4 times larger than those on Flemish Cap and Southeast Shoal for both the along-bank and cross-bank directions. There are suggestions of additionally enhanced excursions: in the near-

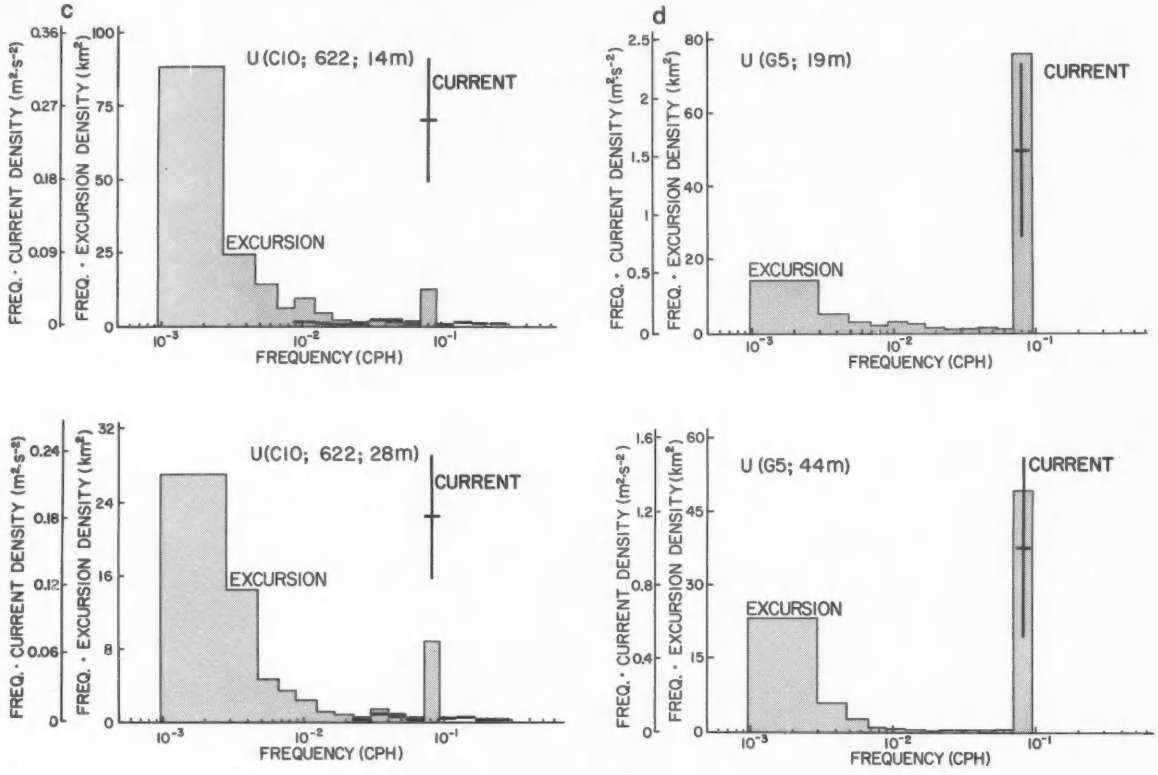

FIG. 6. (*Concluded*)

surface waters for both directions, as on the other banks; in the along-bank direction for all depths on the Bank's plateau (C10); and in winter for the cross-bank excursions in the near-bottom waters on the Bank's side (C4). While the along-bank excursions remain substantially less than the mean-current displacements, the cross-bank excursions are of comparable magnitude to the cross-bank displacements. One significant consequence of the larger excursions on the smaller Browns Bank is that the cross-bank excursion *range* ($2L_c$), particularly near the surface, is of the same order of magnitude as the Bank's and western cap's effective radii (Table 1), suggesting that most water parcels are displaced from the Bank (at least temporarily) on a time scale of about 11 d (one half of the period of lowest-frequency fluctuations considered). Similarly, the near-surface cross-bank excursion range on the Bank's southwestern side is of the same order of magnitude as the minimum separation distance (~40 km) between Browns and Georges Banks (Fig. 1b), suggesting that some interbank exchange may be possible on this time scale. Although the tidal excursions are larger on Browns Bank than on Flemish Cap and Southeast Shoal, the larger excursion standard deviations described above are primarily associated with enhanced current fluctuations at subtidal frequencies (Table 2; Fig. 6c). The dynamical origin of the enhanced low-frequency currents on Browns Bank is uncertain but candidate factors include the monthly and fortnightly variations in the residual current arising from tidal rectification (e.g. Smith 1983), the enhanced response to wind forcing on the forward (western) portion of the Scotian Shelf and in the Northeast Channel region (e.g. Wright et al. 1986), and the impingement on the outer shelf of fluctuating currents associated with the Gulf Stream system (e.g. Smith and Petrie 1982).

The excursion standard deviations at site G5 on the Northeast Peak of Georges Bank are generally of intermediate magnitude between those on Browns Bank and the other banks, although the cross-bank excursions are comparable with the summertime middepth values on Browns Bank. The along-bank excursions are much smaller than the along-bank mean-current displacements, while the cross-bank excursions are about half the cross-bank displacements. The cross-bank excursion ranges are much less than the Bank's radius and significantly smaller than the separation distance from Browns Bank. The strong tidal currents on Georges Bank, particularly in the cross-bank direction, make a greater contribution to the total excursion variance than elsewhere (Fig. 6d), with the peak cross-bank excursion in the near-surface region being at the semidiurnal tidal period.

This first examination of integral space scales for the horizontal circulation on the four northwestern Atlantic banks thus suggests substantial interbank differences which have implications for cross-bank exchange and hence for influences of the physical environment on the banks' biological processes. However, verification of the assumptions in the excursion determinations, computation of excursion spectra for additional sites, and incorporation of the excursion standard deviations into horizontal exchange models are required before the representativeness and implications of these first results can be explored in detail. Rotary coherence analysis on the existing current rec-

TABLE 6. Net displacements by the mean current and total excursion and peak excursion standard deviations for cross-bank (x) and along-bank (y) currents at various sites on the four northwestern Atlantic banks. The mean-current displacements and associated standard errors (shown in parentheses for cases where it exceeds the displacement) are taken as the current means and standard errors from Table 2 times 5.3d (128h), which is one quarter of the longest period resolved in the excursion estimates. Except where indicated otherwise, the peak excursions occur in the lowest frequency band corresponding to a period of 512 h. The nominal seasons of deployment (S = summer; W = winter) are indicated for the Browns Bank records.

Site (mooring number, depth)	Net displacements by mean current (km)		Total excursion standard deviations (km)		Peak excursion standard deviations (km)	
	x	y	x	y	x	y
Flemish Cap						
F1 (322, 54 m)	0 (±2)	9	4	5	4	4
(322, 184 m)	0.9 (±1)	10	3	4	2 (93 h)	2 (256 h)
Southeast Shoal						
S1 (774, 20 m)	11	6	3	6	3	5
(774, 45 m)	8	7	2	3	2	2
Browns Bank						
C4 (326, 14 m) S	0.5 (±15)	51	16	13	12	11
(360, 15 m) W	24	38	12	17	9	13
(326, 49 m) S	5 (±9)	68	7	8	5	5
(360, 50 m) W	6	47	9	14	7	11
(326, 99 m) S	9	20	6	7	5	6
(360, 100 m) W	1 (±3)	26	14	10	11	8
C10 (622, 14 m) S	16	55	11	17	9	14
(667, 15 m) W	12	62	9	18	6	15
(622, 28 m) S	12	50	6	12	5	9
(667, 31 m) W	0.5 (±2)	50	7	14	5	11
(622, 58 m)	9	28	4	8	3	7
Georges Bank						
G5 (—, 19 m)	9	47	6	7	5 (12 h)	4
(—, 44 m)	14	27	6	5	5	3

ords from Browns Bank indicates that there is significant coherence across the Bank (C3–C8) in the low-frequency current fluctuations, consistent with one of the assumptions in the excursion computation, but the assumptions of spatial uniformity in current amplitude and of horizontal coherence on the other banks need investigation.

Discussion and Conclusions

Integral-Scale Approach

The integral space and time scales introduced above may now be used to provide a characterization of circulation and mixing on submarine banks. In particular, the time scales for exchange in three orthogonal directions (around-bank, cross-bank, vertical) can be used to obtain a first assessment of the implications of observed currents for the evolution of scalar fields. The significance of any around-bank residual gyre should be assessed through comparison of the associated recirculation time with the bank's residence time, vertical exchange time, and a time scale for around-bank diffusion. In the limit of the residence time or around-bank diffusion time being much shorter than the recirculation time, for example, a residual gyre may be of little significance to scalar evolution, even though the mean currents may be significantly different from zero statistically. Similarly, in the limit of the vertical exchange time being much shorter than the recirculation time, the significance of vertical structure in the around-bank mean current may be limited. The important points are that the implications of a particular current component should be addressed in relation to currents in other directions and in other frequency bands and that the associated integral scales form a concise quantification of some influences of these currents.

The integral-scale approach may also be used to describe longer-term variability in the physical environment and to examine the significance of the current regime for the distribution of "active" scalars and organisms. For the former, the temporal variability of the integral scales can be examined, as done here for the vertical diffusion distance and time. For the latter, integral space and time scales can be computed from model-predicted distributional changes of particles with a mathematically specified behaviour in a flow field specified on the basis of observed currents.

A First Characterization of the Four Northwestern Atlantic Banks

Figure 7 schematically summarizes the relative redistribution rates implied by the integral time scales for exchange in the three orthogonal directions on the four northwestern Atlantic banks. Although the vertical exchange time is for turbulent diffusion only and the around-bank exchange time for advection only, existing information suggests that the dominant exchange processes are represented (with the possible exceptions of vertical exchange by upwelling on the sides of Georges Bank and by density-driven convection on all four banks in winter and of

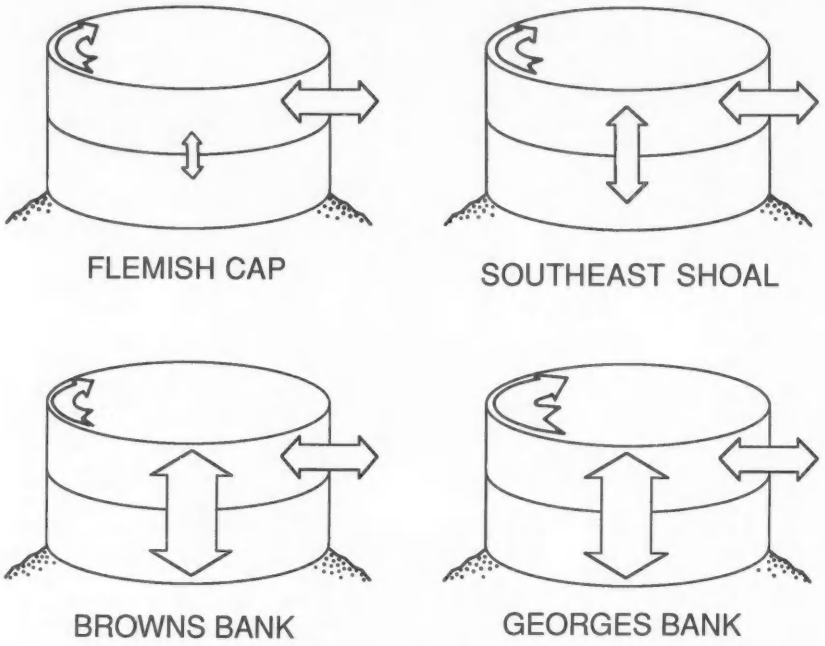

FIG. 7. Schematic summary of the integral time-scale characterization of circulation and mixing on the four northwestern Atlantic banks. The water over each bank is approximated as a two-layer cylinder, and the area of the arrows is inversely proportional to the vertical diffusion time, recirculation time, or residence time, normalized by the residence time for each bank. Thus, only the relative rates of exchange for a particular bank are represented. The Browns Bank characterization is for the whole bank.

around-bank exchange by current fluctuations on Southeast Shoal).

On the relatively deep Flemish Cap, the vertical diffusion time (Table 4) is much longer than the recirculation and residence times (Table 5), implying that passive materials introduced into the Cap's upper or lower layer can generally be expected to leave the Cap in that layer. An intermittent gyre results in the tendency for water parcels to circulate in a clockwise sense around the Cap on average, but since the residence time of near-surface water over the Cap is usually less than the gyre's recirculation time, complete circuits of near-surface water parcels rarely occur. The smaller cross-bank excursions in the near-bottom region (Table 6) suggest that complete circuits may occur more often below the surface layer, but there is little information on the actual residence and Lagrangian recirculation times there. In spite of the limited recirculation on Flemish Cap, the Cap may nevertheless be of sufficient extent that its residence time is favourable to some biological processes, particularly below the surface layer.

The limited current observations from the relatively shallow Southeast Shoal indicate that its vertical diffusion time is comparable with, or smaller than, its residence and recirculation times, ranging from the order of days or less in winter to weeks in summer. There is little evidence for a persistent gyre over the Shoal and, in any case, the apparently short residence time of the near-surface water may render any gyre of limited biological and fisheries significance. On the other hand, the Shoal domain considered here is bounded to the north and west by the extensive Grand Bank which, in many ways, is a similar physical environment to the Shoal itself but has a much longer residence time (e.g. Petrie and Isenor 1985). The principal difference from Flemish Cap which can be identified at this point is the faster and more continuous (on a seasonal basis) vertical exchange.

On Browns Bank the vertical diffusion time is much shorter than the recirculation and residence times, in spite of the Bank's limited horizontal extent and relatively short (compared with the other banks) residence time. Thus, passive materials should generally be redistributed over much of the water column before leaving the Bank. For the Bank as a whole, the recirculation time of the persistent clockwise gyre is longer than the residence time so that complete circuits of the Bank seldom occur here as well, but the recirculation time for the western cap is comparable with the residence time so that more circuits are observed. There is greater low-frequency (periods of days to weeks) current variability on Browns Bank than on the others, such that it is the only one for which the associated average water parcel excursion is comparable with the Bank's horizontal extent.

The vertical diffusion time is also much less than the recirculation and residence times on Georges Bank, although there is a strong horizontal gradient in the former across the summertime tidal front. Averaged over the year, the recirculation time of the well-known clockwise gyre and the residence time are of comparable magnitude, while, in summer, there is a suggestion that the residence time exceeds the recirculation time.

Thus, the Georges Bank gyre can be expected to have a greater influence on spatial patterns than the gyres elsewhere, although it must be emphasized that it is not a "barrier" to cross-bank exchange. The large extent and residence time of Georges Bank may make it more favourable to some biological processes than the other banks considered.

The formulation and application of the integral-scale characterization has also identified gaps in the relevant physical oceanographic database for the banks considered. There are very few measurements of vertical mixing rates on the entire shelf, including banks, and large uncertainties in existing parameterizations of the mixing rates in terms of easily measured quantities. The most extensive database on horizontal currents is from moored measurements, but only for Browns and Georges banks are there measurements at enough sites to approach even a crude integral characterization, particularly for the recirculation time. On the other hand, the cross-bank excursion spectrum and its spectral integrals are properties which can be derived from current measurements at a single site and are relevant to cross-bank exchange on a bank-wide scale. Finally, although Lagrangian drifter trajectories are perhaps the most relevant and easily interpreted observations pertaining to recirculation and residence times, at least for the near-surface region, a considerably larger database is required in order to obtain statistically reliable estimates of these quantities.

Suggestions for Biological Applications

Two general approaches to the use of an integral-scale characterization of circulation and mixing in examining physical influences on biological processes are apparent.

In the first approach, the absolute magnitudes of the physical space and time scales for a particular region can be compared with the observed space and time scales of the biological regime to identify possible linkages. Relevant biological space scales might be the spatial extent of an area of high primary production, the euphotic zone depth, the thickness of the chlorophyll maximum layer, the horizontal extent of a spawning or nursery area, and the range of distribution of a particular stock. Relevant biological time scales might be the time scales of phytoplankton photoadaptation, the doubling times for phytoplankton and zooplankton, the incubation period for fish eggs, the duration of various larval fish stages, and the previously mentioned point of no return for starving larvae. The physical space (time) scales for various processes and for time periods (distances) corresponding to the biological time (space) scales can then be compared with the biological space (time) scales in developing specific hypotheses for environmental influences on the biological phenomenon of interest. In examining such hypotheses, evidence can be sought for long-term biological variability associated with any long-term variability in the matched physical process(es).

The second general approach would be to classify a large number of, say, banks in various multidimensional integral-scale parameter spaces and formulate hypotheses for environmental influences on the basis of similarities in the ecosystem structure of banks lying in particular integral-scale parameter ranges. The parameters could be chosen as either the absolute magnitude of the integral scales, or their magnitude normalized by some fundamental scale (such as the bank radius or residence time) so that the relative importance of various effects could be examined. Such a parametric characterization of the physical environment could also be used to examine existing or independently formulated hypotheses for environmental influences on ecosystem structure. Potential hypotheses might be that banks with short vertical diffusion times have a higher nutrient recycling rate and/or more efficient energy transfer between trophic levels, banks with short residence times have enhanced "new" primary production and/or reduced average recruitment rates, and banks with short recirculation times (relative to residence times) have higher around-bank structure in their ecosystems, particularly between trophic levels.

Clearly, more information, both physical and biological, is required for a proper application of these approaches. However, from a physical oceanographic perspective at least, the integral-scale approach does hold the promise of being a concise and quantitative representation of the relevant environmental variability.

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Seasonal Ingestion Rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario

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Dermott, R., and K. Corning. 1988. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. Can. J. Fish. Aquat. Sci. 45: 1886–1895.

Pontoporeia hoyi in Lake Ontario do not feed continually, their guts averaging 48% full. Feeding intensity of immature amphipods follows the changes in percent of carbon of the settling organic matter, being highest during the late spring and fall. Gut filling time ranged from 6.7 to 3.4 h at 5 and 14°C. Daily ingestion of organic matter ranged from 0.05 $g \cdot m^{-2} \cdot d^{-1}$ at the deepest station sampled (125 m) to 0.17 $g \cdot m^{-2} \cdot d^{-1}$ at the shallowest (35 m). The organic matter ingested by the *Pontoporeia* present represented 8.8 and 7.9% of the average daily rate of organic matter deposited at these two stations respectively. The lakewide estimate of the organic matter consumed by *Pontoporeia* in Lake Ontario was about 19 $g \cdot m^{-2} \cdot yr^{-1}$ during 1981 and 21 $g \cdot m^{-2} \cdot yr^{-1}$ during 1982.

Les *Pontoporeia hoyi* du lac Ontario ne s'alimentent pas de façon continue, leur intestin n'étant, en moyenne, plein qu'à 48 %. L'intensité de l'alimentation des amphipodes immatures se conforme aux variations du pourcentge de carbone de la matière organique qui sédimente : elle est le plus élevé au cours de la fin du printemps et à l'automne. Le temps nécessaire au remplissage des viscères variait de 6,7 h à 5°C, à 3,4 h à 14°C. L'ingestion quotidienne de matière organique variait de 0,05 $g \cdot m^{-2} \cdot d^{-1}$ à la station la plus profonde (125 m), à 0,17 $g \cdot m^{-2} \cdot d^{-1}$ à la station la moins profonde (35 m). La matière organique ingérée par les *Pontoporeia* représentait, respectivement à ces deux stations, 8,8 et 7,9 % du taux quotidien moyen de la matière organique consommée par les *Pontoporeia* dans l'ensemble du lac Ontario s'élevait à 19 $g \cdot m^{-2} \cdot a^{-1}$ en 1981, et à 21 $g \cdot m^{-2} \cdot a^{-1}$ en 1982.

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The amphipod *Pontoporeia affinis* (Lindstrom) or its Nearctic analog *Pontoporeia hoyi* (Sars) is the principle benthic organism of most large lakes in previously glaciated regions of the Holarctic. In the Great Lakes, *P. hoyi* (possibly composed of several species, E. L. Bousfield, National Museum, Ottawa, Ont., pers. comm.) populations are greatest on soft sediments or fine sands with organic coatings (Marzolf 1965a) at depths where temperatures remain below 14°C (Dadswell 1974). The abundance, body size, and high lipid content of this deposit-feeding amphipod makes it very important in the transfer of carbon as well as chlorinated organic contaminants from the sediments to the fish communities (Juday and Birge 1927; Ankar 1977; Gardner et al. 1985). To assess the transfer of energy or contaminants through the populations, basic knowledge of production, respiration, and feeding rates of the species is required. Work has been completed on production, respiration, and calculated assimilation for *Pontoporeia* spp. (Johnson and Brinkhurst 1971; Cederwall 1977), but little has been done on the feeding rate of this burrowing amphipod.

We examined the seasonal feeding intensity and the relationships between the ingestion rate of *P. hoyi* with water temperature and body size. Seasonal ingestion rates were calculated from the prevailing temperatures, abundance, and size frequencies of three populations of *P. hoyi* inhabiting different depths in Lake Ontario. Particular emphasis was placed on determining the amount of organic matter ingested by the species, compared with the sedimentation rates at the study sites (Rosa 1985).

Methods and Materials

Sample Collection and Size Frequency

Pontoporeia were sampled from March 1981 to April 1983 at three sites in Lake Ontario used by Environment Canada in their long-term surveillance program. Site 93 (70 m) is situated 20 km east of the Niagara River mouth. The midlake site 41 was 125 m deep, while site 81 (35 m) was situated in the centre of the more productive eastern basin of Lake Ontario (Table 1).

Five replicate Ponar samples (530 cm^2) were collected at each site at approximately monthly intervals from March until November. At the same time, temperature at the bottom was measured using an electronic bathythermograph (EBT) trace to the bottom. The Ponar samples were sieved immediately (mesh 0.21 mm) with the residues containing *Pontoporeia* preserved in 10% formalin. Samples of the surficial sediment (top 1 cm) were analysed three times per year for percent sand and organic content (as loss on ignition at 500°C for 24 h).

In the laboratory, the *Pontoporeia* were removed from the sediment residues. Lengths were determined under a stereoscope to the nearest 0.1 mm, measured as an arc from the base of the antenna to the base of the telson. Numbers in each 1-mm size class (i.e. 2.0–2.9 mm) were enumerated, with each Ponar sample being treated separately. The animals were

TABLE 1. Sample locations (east to west), depth, and sediment characteristics with 95% confidence intervals.

Site	81	41	93
Latitude	43°58.9′	43°43.0′	43°21.8′
Longitude	76°39.3′	78°01.6′	78°51.4′
Depth (m)	35	125	70
Bottom temperature			
Maximum (°C)	12.4	4.2	7.0
Minimum (°C)	0.4	1.4	1.2
Sediment texture	Sandy clay	Silty clay	Sandy silt
Grain size (ϕ units)	5–7	8	3–5
% sand	1.26 ± 0.18	0.65 ± 0.04	7.63 ± 1.84
% organic content	10.49 ± 1.65	9.71 ± 0.90	5.97 ± 1.17

then grouped as three sizes representing different cohorts, hatchlings (<2 mm) plus the young of the year (YOY) (<4 mm), immature juveniles (4–6 mm), and adult size (>6 mm) and represerved. The gravid and spent females in each sample were counted. Abundance of the smallest size class (<2 mm) was estimated from the number of eggs carried by the gravid females during the previous month assuming a 50% mortality. The average gut fullness was calculated for each of the three size cohorts by also measuring the length of the gut material and total gut length of subsampled animals from only the first two replicate samples of the five Ponar grabs taken each date.

Additional Ponar samples were collected during May and October and maintained unsieved at the temperature recorded near the bottom. Live animals removed from the mud were anaesthetized with cold soda water and their lengths measured to the nearest 0.1 mm. Their dry weights were estimated to the nearest 0.01 mg after drying for 24 h at 60°C in order to calculate the length – dry weight relationships for the populations at each of the three sites. Additional specimens with full guts were used to calculate the body length – gut volume relationships, as well as their gut content weight and organic content of the gut material. After measuring body length and volume of the gut contents, the gut contents were dissected out, retained on 0.5-μm glass fibre filters, dried, and weighed. The percent organic content of the gut contents was calculated as loss on ignition at 500°C for 12 h.

Ingestion Rate by Visual Observation

Attempts were made to measure the feeding rate using ^{14}C-labeled algae mixed into the sediment (Hargrave 1970; Dermott 1981). However, highly variable radioactive counts on non-feeding controls, due to ^{14}C adsorption onto or between the body segments, prevented calculation of ingestion by this method. Therefore, ingestion by *Pontoporeia* was determined by measuring the percentage of gut length which possessed sediment after the amphipods had burrowed in sediment for a set time at 5, 10, and 14°C. To maximize the number of animals feeding, only amphipods with previously filled guts were used in the experiments. Cultures of *P. hoyi* were kept at the test temperatures for 3–14 d after collection. Animals with full guts were placed in submerged chambers having a bottom of 1.0-mm screening and allowed to purge their guts over 12–18 h in the dark. Any fecal pellets produced (<0.3 mm in diameter) passed through the mesh, preventing reingestion. Fresh sediments from the same collection sites as the test animals were gently sieved through a 0.25-mm mesh to remove organisms and larger detritus. Portions of this sediment were added to feeding chambers made from Plexiglas cylinders (7 × 13 cm) with a 1.0-mm screen bottom, inserted into 700-mL jars. The jars were filled with aerated water and the sediment allowed to settle over 12 h, leaving approximately 2 cm of sediment above the mesh.

The *P. hoyi* with purged guts were then transfered to the sediment in the feeding chambers using a wide-mouthed pipette. Care was taken to keep the amphipods submerged, as air trapped under the coxal plates entraps the animals at the water surface. Ten to 12 similar sized animals (range 3–8 mm) were added to each feeding chamber, the surface covered with 1.0-mm mesh. The feeding chambers were incubated in the dark over a 4- to 6-h period, with a chamber removed at intervals ranging from 0.5 h at 14°C to 1 h at 5°C. The mud was sieved through the meshed bottom of the cylinder, and the cylinder was transferred into 25% soda water mixed with cold water to narcotize the amphipods.

The narcotized *P. hoyi* were examined under a stereoscope, with body length, percentage of the gut length filled with sediment, and gut content volume measured using an ocular micrometer. Regression lines were used to extrapolate the gut filling time (GFT) required for the guts to become 100% full at 5, 10, and 14°C. The ingestion rate (milligrams per animal per hour) was estimated at the three test temperatures from the gut content volume present at the end of each time interval. The gut content volume was converted to dry weight using the density of the gut contents (0.614 ± 0.053 $mg \cdot mm^{-3}$) measured previously. Regressions between amphipod length and ingestion rate were calculated for each of the three test temperatures, with over 70 amphipods used at each feeding temperature. A multiple regression for ingestion at all temperatures was also calculated using amphipod lengths and temperatures.

The theoretical maximum ingestion rates (milligrams per square metre per day) of the three populations were calculated from the population densities, size frequencies, and monthly bottom temperature at each of the three sites. The organic matter of the gut contents changed with amphipod size; therefore, monthly ingestion rates were calculated separately for the YOY (<4 mm), juvenile, and adult (>6 mm) size cohorts. The actual ingestion rates by each of these size cohorts were corrected for the average gut fullness of that cohort measured in the monthly samples from Lake Ontario.

Results

The minimum and maximum bottom water temperatures at the three sites sampled are listed in Table 1. The shallow eastern end of Lake Ontario (site 81) is the only portion of the lake

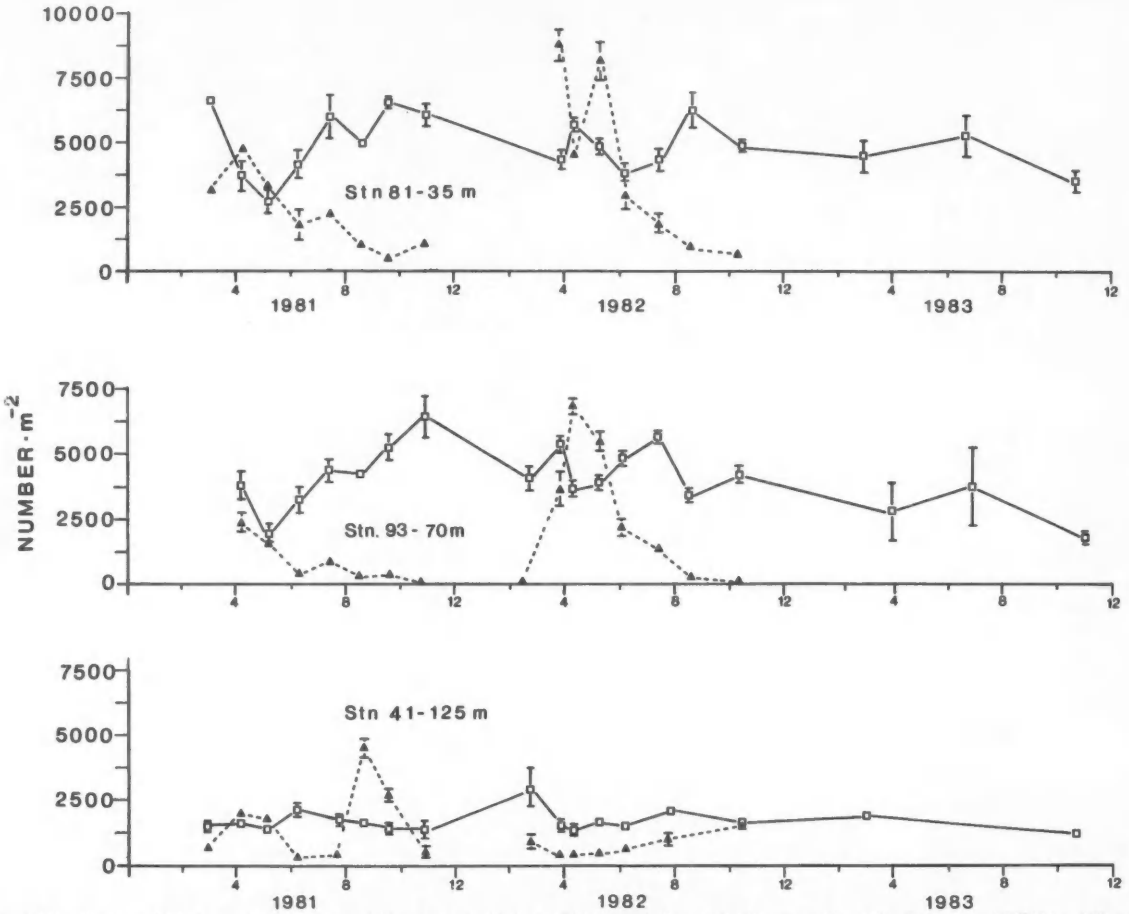

FIG. 1. Populations of *Pontoporeia* at the three stations in Lake Ontario. Total population (solid line) as collected in Ponars, and YOY hatchlings (broken line) collected or calculated from the number of eggs produced. Vertical bars represent ±2 SE.

that regularly freezes during winter. The bottom temperature at site 93 (70 m) reaches its maximum in late October during the fall overturn. Sediments at all three sites were silts or clay, with the finest sediment occurring at the deepest site. The higher sand content at site 93 reflects the influence from the Niagara River, 20 km westward, as well as its proximity to the shoreline, 3 km to the south. The organic content of the surface sediments (Table 1) displayed no significant seasonal changes (ANOVA, $p > 0.1$).

Abundance and Biomass

The size frequencies of *P. hoyi* indicate a 2-yr life cycle, with three cohorts present during the spring. The YOY normally are released from the brood pouches of the gravid females during early spring. Unlike the populations at the two shallower sites, peak release of the young at site 41 (125 m) occurs during August, with a minor period of reproduction during April. The total populations depicted in Fig. 1 do not include the number of young hatched (broken line) from the eggs produced by the females.

At the two shallower sites, where reproduction occurs during the spring, population abundance was lowest in early summer (Fig. 1) due to mortality of the adult females. The apparent rise in population during July was possibly due to inefficient collection of the YOY before they reach a length of about 2.6 mm. Incomplete collection of the young was not a result of the sieve used, as the average egg diameter at hatching (0.62 ± 0.08 mm) would be retained by the 0.21-mm mesh used. At the two shallow sites, the YOY were adequately sampled between July and November (1981–1982), average densities during these months were 5875 ± 406, 5097 ± 782, and 2990 ± 941·m^{-2} at site 81, 93, and 41, respectively. Analysis of variance (ANOVA) and Student–Newman–Keuls (SNK) comparisons confirmed that the population of *Pontoporeia* was smaller ($p < 0.01$) at the deeper site 41 than at the other two sites. At the two shallower sites, there were greater seasonal differences ($p < 0.01$) than differences between sites. Seasonal difference was greater at site 93, where the population was slightly greater during the fall of 1981 than during the spring ($p < 0.05$).

Amphipods from the midlake site (41) weighed less than similar size animals at the other two sites. Males of *P. hoyi* var. *brevicornis* at this site were visibly smaller than the males from the other sites. Length–weight regressions revealed a greater weight at any given size (covariance analysis, $p < 0.01$) at the Niagara site (93) than at site 81, so separate regressions were used for each site:

TABLE 2. Interval and daily ingestion (I) of dry sediment, organic matter, and percent of sedimented organic matter ingested by the average *Pontoporeia* biomass at three stations in Lake Ontario with 95% confidence intervals. Maximum ingestion (Max Ing) by *Pontoporeia* assumes continuous feeding for 24 $h \cdot d^{-1}$ each month. OTM = organic trapped matter (loss on ignition) in sediment traps, April – November 1981; OMI = organic matter ingested.

Site	Interval (d)	Biomass ($g \cdot m^{-2}$)	Ingestion ($g \cdot m^{-2} \cdot yr^{-1}$)	Daily I ($g \cdot m^{-2} \cdot d^{-1}$)	OMI ($g \cdot m^{-2} \cdot yr^{-1}$)	Daily OMI ($g \cdot m^{-2} \cdot d^{-1}$)	Sediment OTM ($g \cdot m^{-2} \cdot d^{-1}$)*	% daily OMI:OTM	Max Ing ($g \cdot m^{-2} \cdot d^{-1}$)	Max OMI ($g \cdot m^{-2} \cdot d^{-1}$)
					1981 (March 1981 – March 1982)					
81	393	3.05 ±0.26	285.861 ±18.573	0.727 ±0.047	67.914 ±3.879	0.173 ±0.010	2.2	7.86	1.673 ±0.150	0.395 ±0.034
93	358	2.24 ±0.43	170.736 ±16.532	0.477 ±0.046	41.530 ±3.529	0.116 ±0.010	2.416 ±1.193	4.80	0.972 ±0.106	0.231 ±0.015
41	360	0.99 ±0.18	75.465 ±3.632	0.209 ±0.010	18.388 ±0.818	0.051 ±0.002	0.577 ±0.152	8.84	0.522 ±0.036	0.124 ±0.007
					1982 (March 1982 – April 1983)					
81	352	2.59 ±0.20	210.170 ±21.782	0.597 ±0.062	51.011 ±5.097	0.145 ±0.014			1.289 ±0.148	0.313 ±0.031
93	389	2.42 ±0.21	213.226 ±20.380	0.548 ±0.052	52.344 ±4.986	0.135 ±0.128			1.044 ±0.091	0.253 ±0.020
41	385	0.75 ±0.13	100.047 ±7.715	0.260 ±0.020	24.327 ±1.833	0.063 ±0.005			0.463 ±0.027	0.112 ±0.006

*from Rosa (1985) and Rosa et al. (1983).

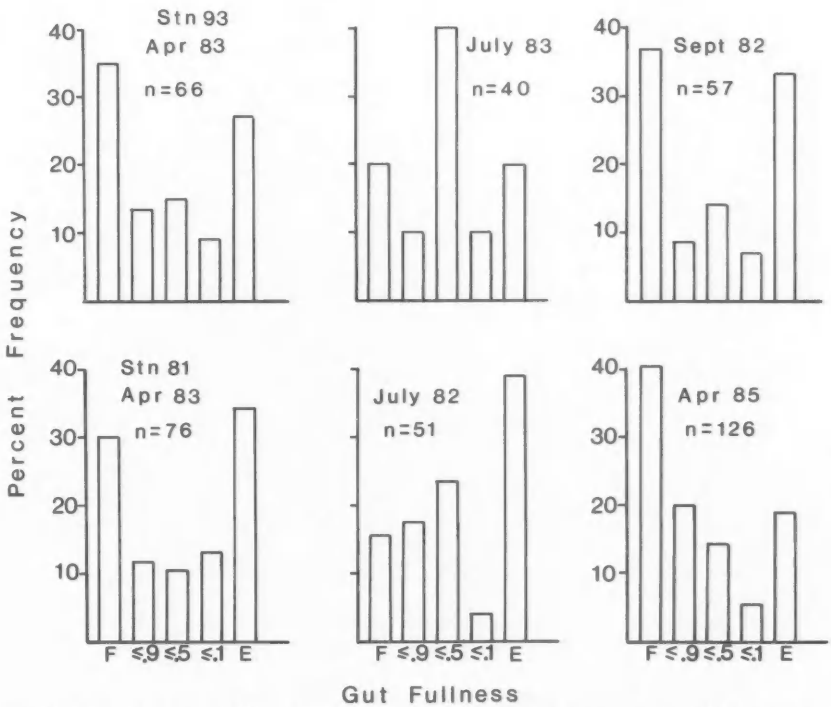

FIG. 2. Percent frequency of 4- to 6-mm *Pontoporeia* having guts in five categories of fullness: F = full; between 0.9 and 0.5 full; between 0.5 and 0.1 full; less than 0.1 full; and E = completely empty. Upper set from station 93, lower set from station 81, n = number of animals examined.

(1) Site 81: mg dry wt. = $e^{(-5.399 + 2.846 \ln \text{length (mm)})}$ $r^2 = 0.90$

(2) Site 93: mg dry wt. = $e^{(-5.468 + 2.963 \ln \text{length (mm)})}$ $r^2 = 0.92$

(3) Site 41: mg dry wt. = $e^{(-6.199 + 3.206 \ln \text{length (mm)})}$ $r^2 = 0.96$.

The biomass present at each site was calculated from the size frequencies at each site and the weight regressions (equations

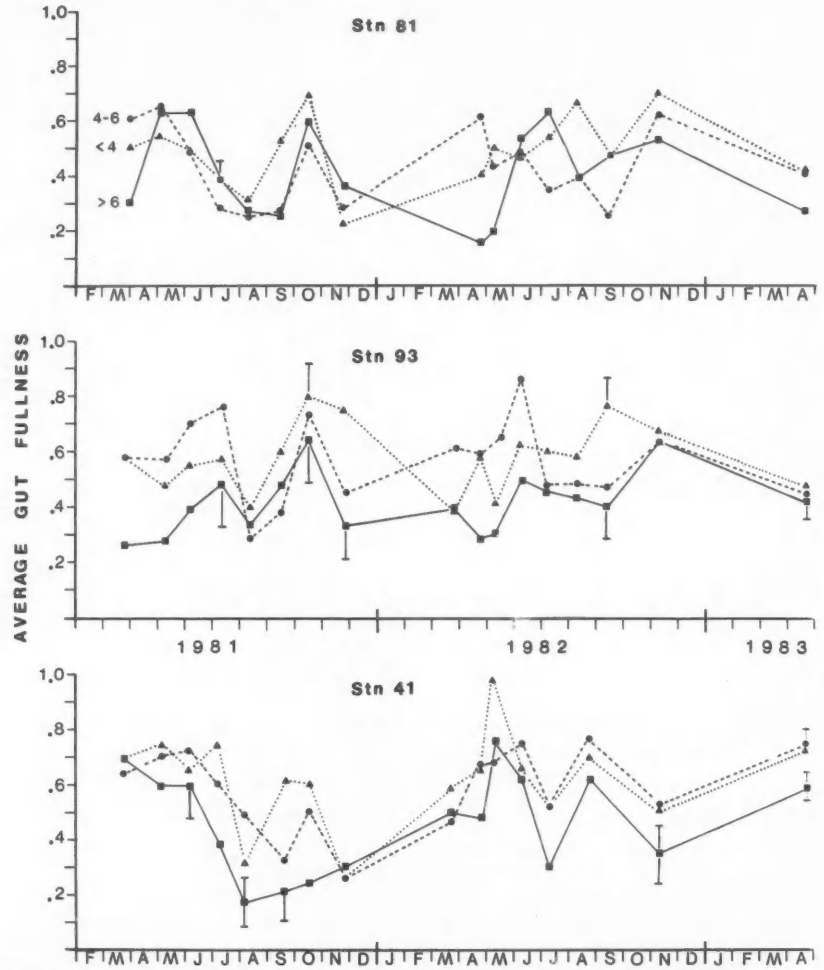

FIG. 3. Seasonal changes in the average gut fullness of the three size classes of *Pontoporeia* in Lake Ontario between March 1981 and April 1983. Partial interval bars represent 2 SE.

1–3). Biomass remained more constant throughout the year than did abundance, with the greatest proportion of the total biomass due to the immature 1 yr old cohort (4–6 mm sizes). The contribution of the YOY cohort to the total biomass at each of the sites was minor. Maximum dry biomass was 3.4 $g \cdot m^{-2}$ at site 81, 3.3 $g \cdot m^{-2}$ at site 93, but only 1.4 $g \cdot m^{-2}$ at the deeper site 41. Average biomass at the sites (Table 2) reflects these differences. Annual differences in biomass occurred only at site 81, where the 1981 biomass was greater than that in 1982 (*t*-test, $p < 0.05$).

Seasonal Variation in Gut Fullness

The majority of *P. hoyi* collected in the field or maintained in the laboratory had either completely full or completely empty guts, indicating that feeding by *Pontoporeia* is not continuous. Although animals could fill their guts within 6 h, approximately 16% of the animals had empty guts after burrowing in their native sediments for 24 h. When placed onto the sediment, all animals except those that became trapped at the water surface immediately burrowed below the mud surface. Gut clearance experiments revealed that as the guts emptied, often the last two to three abdominal segments were also empty. If the high percentage of empty guts in the field samples had been the result of regurgitation and defecation during sampling, material would have been present near the midgut, while the fore and rear guts would have been empty. Few amphipods were found with material only in the midguts. The nonnormal distributions of the frequency of gut fullness in immature amphipods during various dates are illustrated in Fig. 2. On any sample date, a substantial number of the amphipods had empty or partially full guts. Averaged over the whole study period, 26.7 ± 4.78% of the immature amphipods examined ($n = 3115$) had guts that were between 10 and 90% full, the rest having guts that were either almost full or empty.

The average percent of gut fullness in the cohorts was highly variable over the year (Fig. 3). The percentage of full guts was generally highest during the late spring and again in the fall. For the largest size (>6 mm), the percentage of full guts was lowest during early spring at sites 81 and 93, but lowest in midsummer at site 41, due to the high proportion of nonfeeding

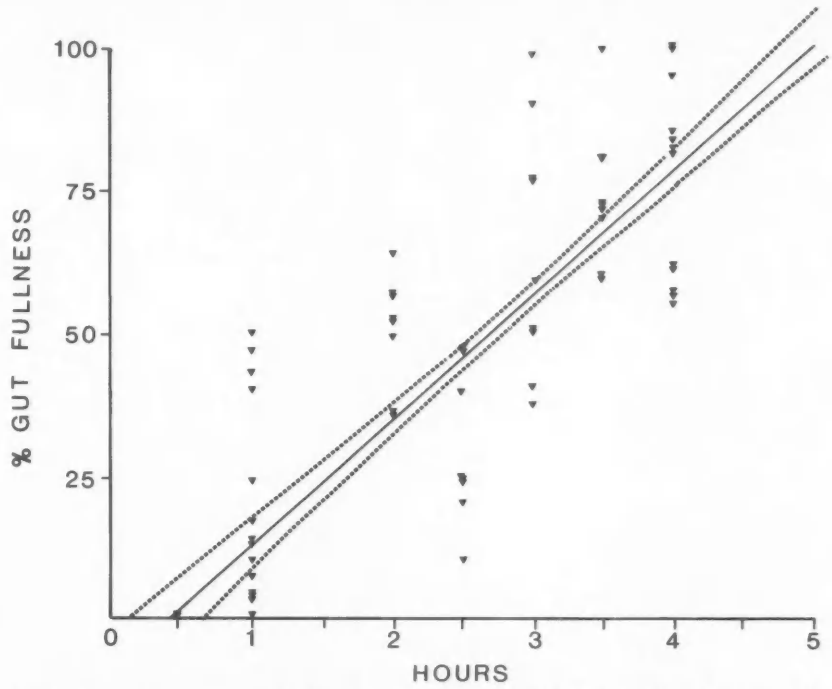

FIG. 4. Time series of percent gut fullness in *Pontoporeia* feeding in Lake Ontario sediments at 10°C. Broken lines represent 95% confidence limits to the regression line $y = 22.08x - 8.94$.

gravid females (up to 14% of the >6 mm cohort). The average percent of gut fullness in the YOY (<4 mm) cohort displayed similar seasonal trends as the immature cohort, with gut fullness ranging from 38 to 98% full (Fig. 3).

Ingestion Rates

Regressions between the percent of gut fullness and feeding interval resulted in GFT of 6.68 ± 1.14, 4.94 ± 0.64, and 3.43 ± 0.51 h at 5, 10, and 14°C respectively for amphipods which fed immediately after burrowing into the sediment. The regression between gut fullness and feeding interval at 10°C is shown in Fig. 4. There was no difference (ANOVA, $p < 0.2$; SNK) in GFT with amphipod size over the sizes measured (3–8 mm). Dry weight of the gut contents was related to the natural log (ln) of amphipod length and was calculated from the regression

(4) Gut contents (mg) $= e^{(-7.232 + 2.753 \ln \text{body length (mm)})}$ $r^2 = 0.89.$

The relationship between ingestion rate (maximum, assuming continuous feeding 24 h·d^{-1}) and amphipod length at all temperatures (T, degrees Celsius) was best described by the following multiple regression:

(5) Ingestion (mg·h^{-1}·animal^{-1}) $= 0.001\, e^{(-2.986 + 0.106T + 2.831 \ln \text{length (mm)})}$ $r^2 = 0.61.$

When the monthly temperatures were within 1°C of that in the feeding experiments, the specific feeding regressions used to calculate ingestion at each temperature were

(6) 5°C: (mg·h^{-1}·animal^{-1}) $= e^{(-8.973 + 2.684 \ln \text{length (mm)})}$ $r^2 = 0.78.$

(7) 10°C: (mg·h^{-1}·animal^{-1}) $= e^{(-10.070 + 3.434 \ln \text{length (mm)})}$ $r^2 = 0.66.$

(8) 14°C: (mg·h^{-1}·animal^{-1}) $= e^{(-8.493 + 2.911 \ln \text{length (mm)})}$ $r^2 = 0.67.$

As the amphipods were not feeding continually, the average percent of gut fullness (Fig. 3) was used to calculate the amount of sediment being ingested by the populations at each sample date. The ingestion rate is also dependent on the temperature as well as the size frequency (equations 5–8) and population size (Fig. 1) present on each sample date. The total amount of dry sediment (grams per square metre per day) ingested by the *P. hoyi* populations was generally highest during the late spring and fall of both years (Fig. 5).

The weight of the full gut contents varied from 15.3 ± 2.8% of the body weight in small (2–4 mm) amphipods to 14.5 ± 1.0% in the larger >6 mm size. Correcting for the average gut fullness of the collected amphipods, small *P. hoyi* had slightly greater ingestion rates per body weight than larger amphipods. The average ingestion rate at site 93 between August and November was 35% body weight·d^{-1} for the 2–4 mm size and 20% body weight·d^{-1} for the larger amphipods (>6 mm), which displayed a reduced average gut fullness (Fig. 3).

The organic content of the material in the whole-gut content was greater in the YOY *P. hoyi* (range 35–41%) than in the immature (4–6 mm) and adult-sized (>6 mm) amphipods, which averaged 25.3 ± 0.8 and 22.9 ± 1.0% respectively during the spring and 24.5 ± 1.06 and 21.9 ± 1.89% during the fall. The average organic content of the gut contents for the

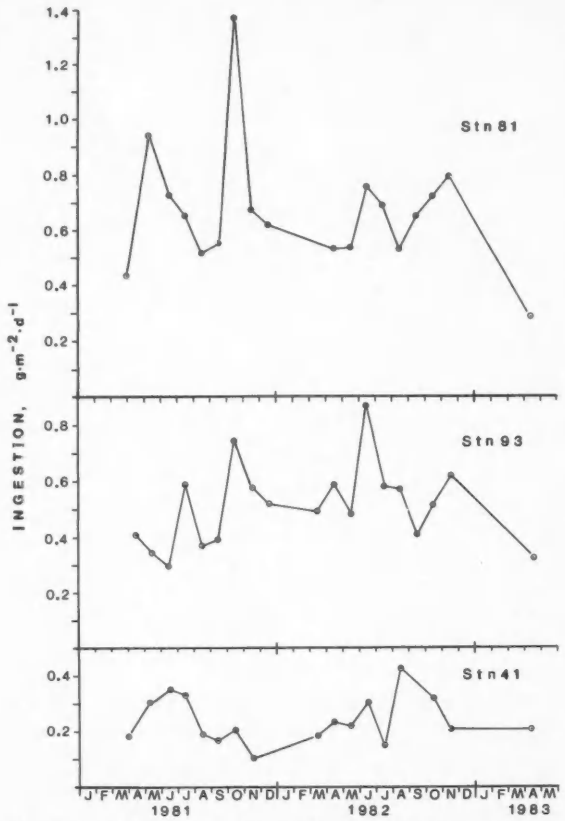

FIG. 5. Total daily ingestion (dry sediment) by the *Pontoporeia* populations present at the three stations in Lake Ontario between March 1981 and April 1983.

YOY, yearling, and adult-sized *P. hoyi* over the sample period, was 38.6 ± 1.6, 24.9 ± 0.6, and 22.4 ± 0.4% respectively. During the fall, the average organic matter of the fecal pellets produced by amphipods of 4–7 mm length was 19.83 ± 1.83%, having a density of 0.516 mg·mm^{-3} (wet volume). In contrast, the organic content of the sediments at the three sites was much lower (Table 1), indicating a high degree of selection of fine particles from the most recently settled sediments.

Ingestion and Sedimentation Ratios

Total ingestion by the *P. hoyi* at site 41 (125 m) between March 1981 and March 1982 amounted to 75.46 g dry weight·m^{-2}, with a mean of 0.21 ± 0.01 g·m^{-2}·d^{-1} (Table 2). This daily ingestion rate is corrected for the average gut fullness of the amphipods. Ignoring the intermittant feeding by *P. hoyi*, the maximum daily ingestion by the *Pontoporeia* population at site 41 would have been 0.522 g·m^{-2}·d^{-1} during 1981 (Table 2), assuming each amphipod fed continuously. The down flux of total particulate matter collected 5 m off the bottom at site 41 (during April – November 1981) averaged 2.20 g·m^{-2}·d^{-1} (Rosa 1985). Most of the sedimentation at the mid-lake site is due to particulate matter produced in the epilimnion (Rosa 1985). During the 1981 sample period, *P. hoyi* consumed 0.05 g organic matter (OMI)·m^{-2}·d^{-1} at site 41 (125 m), which was 8.8% of the average daily organic matter deposited (OTM) at the site (Table 2). During summer, the proportion of OMI ingested ranged between 5 and 24% of the average daily organic matter trapped (OTM) each month at site 41. This ratio was highest in June and remained above 14% in May and July. By August 1981, this ratio (OMI:OTM) dropped to 5% but rose to 9% in October.

The monthly average particulate organic nitrogen (PON) varied from 3.8 to 7.4% of the daily OTM at site 41, while at the more unstable site 93, this average was 0.5–6.7% (Rosa 1985, and unpubl. data). The intensity of feeding at site 41 (indicated by the average gut fullness) suggested good correlation with the percentage of organic carbon or percentage of PON in the OTM (Fig. 6). These relationships at the inshore site 93 were masked by sediment resuspension that occurs at that site by physical mixing, especially during fall overturn (Rosa 1985).

Sedimentation at the two shallower sites was much greater than at midlake, with a mean sediment flux of 11.0 and 17.5 g·m^{-2}·d^{-1} occurring at sites 81 and 93 respectively, containing a mean organic content of 20 and 17% (Rosa et al. 1983; Rosa 1985). During 1981, the OMI of the *P. hoyi* population at site 81 (35 m) was 0.17 g·m^{-2}·d^{-1}, or 7.9% of the daily OTM (Table 2). Total ingestion by the *P. hoyi* at site 93 between March 1981 and March 1982 amounted to 171 g·m^{-2}·yr^{-1} (Table 2), with 0.12 g OMI·m^{-2}·d^{-1}. This ingestion represented 4.8% of the average organic matter settling daily in 1981.

The ratio of daily OMI of the *P. hoyi* population at inshore site 93 to the average daily OTM each month ranged between 3 and 66% (F. Rosa, unpubl. data). The highest ratio occurred in April, during a period of very low sedimentation at this site (0.15 g·m^{-2}·d^{-1}). Formation of a strong thermal bar along the shore in April entraps much of the material entering from the Niagara River close to the shore. During the other months, this ratio (OMI:OTM) averaged only 3.2% at site 93. The input of organic matter from the Niagara supports a large *P. hoyi* population at site 93, in excess of 5000·m^{-2}.

The daily ingestion rates during 1982 at the two deeper sites were greater than in 1981. Changes in the average daily rates were due to differences in average population biomass present (Table 2), as well as changes in the percentage of amphipods with full guts (Fig. 3). The latter was responsible for the increased ingestion at site 41, in spite of a reduced biomass in 1982.

Discussion

Sediment Selection

Detritivores are able to detect differences in substrate composition and are often highly selective in the sediment they inhabit. *Pontoporeia* spp. require a sediment into which they can burrow (Smith 1972), selecting fine sediments containing high bacterial numbers (Marzolf 1965a) or sandy sediments with a thin layer of fine detritus. Feeding is presumed to occur below the sediment – water interface and we saw no feeding animals on the sediment surface in our laboratory. Although the surface quickly becomes well mixed down to 1.5 cm by the activities of the amphipods, few obvious burrow openings were visible in cultures containing over 3500 animals·m^{-2}. The tilling activity of the amphipods was restricted to a narrow layer below the sediment surface. Both Milbrink (1973) and Heuschele (1982) found *Pontoporeia* spp. most abundant in the top 2 cm of lake sediments.

Substrate selection by *Pontoporeia* is similar to that by the marine burrowing amphipod *Corophium* (Meadows 1964);

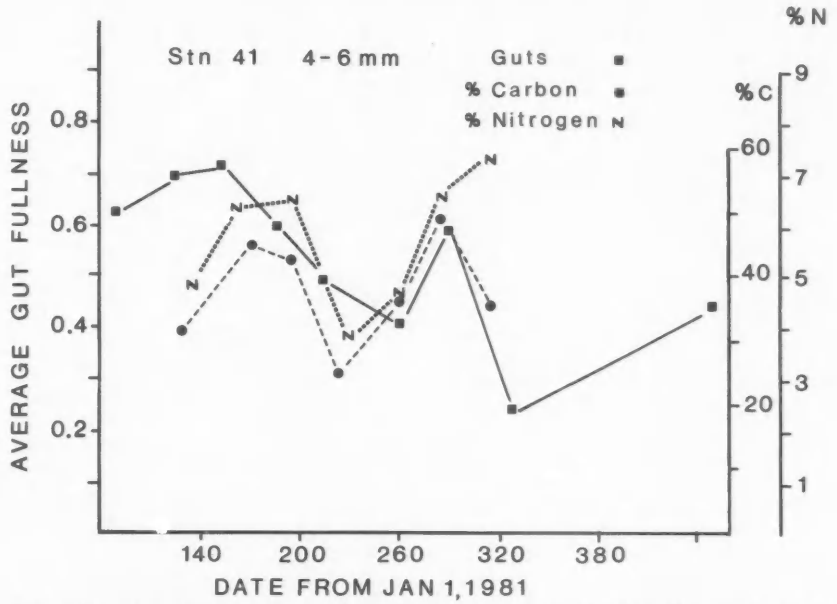

FIG. 6. Average gut fullness of the 4- to 6-mm *Pontoporeia* at station 41 during 1981, compared with the percent of particulate organic carbon and percent of particulate organic nitrogen in the settling organic matter (from Rosa 1985, and unpubl. data).

however, there is no evidence that *Pontoporeia* construct permanent U-shaped burrows. As with *Corophium volutator* (Fenchel et al. 1975), *Pontoporeia* are highly selective in the size of the particles ingested. Ankar (1977) and Moore (1977) found feeding *Pontoporeia* spp. to be size selective, with the majority of particles ingested being <10 μm. The maximum particle size ingested was 50–60 μm, while sand grains (100 μm) in the sediments were not ingested. Algae represented only 1–2% of the gut contents, with most of the predominant planktonic species being ingested in proportion to their abundance (Moore 1977; Johnson 1987). The elevated organic content of the gut material over that of Lake Ontario sediments (2–4 times) indicates selection of particles on the basis of their size or organic content. There was close agreement between the average organic content of the gut material in the larger amphipods (22–25%) and that of settling particles trapped 5 m off the bottom, which had organic contents of 20 and 26% at sites 81 and 41 respectively (Rosa et al. 1983; Rosa 1985). The burrowing mayfly *Hexagenia limbata* displays a similar selection of organic particles (Zimmerman and Wissing 1978), with the precentage of organic matter ingested closely matching that of the most recently settled particles. Many detritivores are able to select food quality and adjust food intake to optimize their energy return (Cammen 1980).

Seasonal Gut Fullness

The calculated ingestion rates for *P. hoyi* are conservative, assuming intermittant feeding with an average gut fullness of only 48%. Variable feeding intensity has been observed in *Pontoporeia* spp. (Moore 1977 and 1979; Semenchenko 1979; Johnson 1987; Quigley 1988). Moore (1979) noted that relatively few *P. hoyi* (5–10%) in Great Slave Lake contained material in their guts during winter, regardless of size, and found a strong correlation between light (photoperiod) and the percentage of animals feeding, which may have been coincidental. In Great Slave Lake, the cessation of feeding (Moore 1979) may have been in response to the availability of phytoplankton under the ice during the subarctic winter, rather than actual photoperiod.

Mature males and gravid females feed sparingly; however, they only occur seasonally and account for <40% of the 6–10 mm size class during spring when feeding activity is greatest. Reduced feeding by the reproducing and dying postreproductive amphipods was responsible for the low percent gut fullness of the adult-sized cohort during the brief period of reproduction. However, reproduction is not responsible for the low feeding activity of the abundant immature or YOY amphipods during the summer. Molting causes a cessation of feeding by *Hyalella azteca* and *Gammarus pulex* for an 18- to 24-h period (Hargrave 1972; Willoughby and Earnshaw 1982). If *Pontoporeia* have the same number of instars as *H. azteca* (Geisler 1944) during their life span, molting would occur 8–12 times. This would only reduce the number of *P. hoyi* feeding each month by about 2%, not the 30–70% reduction observed (Fig. 3). Whatever the reason for the cessation of feeding by individual *P. hoyi*, ingestion is not continuous, but occurs intermittently.

Lateral movements in the sediments and nocturnal swimming activities off the bottom (Lindstrom and Lindstrom 1980) will cause periodic cessation of feeding until subsequent reburrowing. Vertical migration by *P. hoyi* in the Great Lakes has been documented (Wells 1968); however, Marzolf (1965b) reported that less than 7% of the populations undergo vertical migration during nighttime. No change in feeding intensity during day or night was evident in the samples collected in Lake Ontario. However, closer examination of diurnal feeding rate is warranted, since the samples examined were collected at monthly

intervals, rather than during a limited period. Seasonal changes in ingestion rate would be expected if the amphipods respond to changes in the quality of the settling particles. The number of animals feeding was greatest during the spring and fall, in response to the quality (high percent N and P) of settling detritus from the spring and fall blooms of diatoms (Johannsson et al. 1985). Similarily, Quigley (1988) found the feeding activity of *P. hoyi* in Lake Michigan to be highest in spring and low during summer.

Seasonality of Energy Uptake

Variable phytoplankton production and subsequent sedimentation throughout the summer results in changes to both the availability of food and its quality. Large blooms of diatoms occur in Lake Ontario during March–June (Johannasson et al. 1985), followed by Chrysophyceae and Crytophyceae during summer. The large diatoms settle rapidly, whereas in midsummer, there is appreciable retention of particulate matter in the thermocline (Rosa 1985). Reduced quality of the settling particles occurs in summer, as the organic carbon in the seston of Lake Ontario drops from 15 to 5% of the total suspended matter between spring and summer (Rosa 1985), largely due to $CaCO_3$ precipitation in summer. The relative role of algae, bacteria, and detrital aggregates in the energy supply of *P. hoyi* changes with seasonal cycles of production and decomposition in Lake Ontario. However, there are indications that the diatom blooms are a major food resource for *Pontoporeia*.

A rapid increase in the lipid content of Lake Michigan *P. hoyi* occurs between April and June (Gardner et al. 1985), in conjunction with the spring diatom bloom. Amphipods are capable of rapidly accumulating lipids in response to increased food (Clarke et al. 1985). Diatoms are efficiently digested by benthic invertebrates (McCullough et al. 1979; Stuart et al. 1985). In addition, their rapid settling rate and high lipid content (Lewin and Guilland 1963) result in high-quality food being abundant during early summer. The amphipods at the midlake station in Lake Ontario ingested a much greater proportion of the settled organic matter during June than at other times of the year, implying that the debris from the spring diatom bloom is a preferred food source. This is reflected in that growth rates of both the YOY and immature *Pontoporeia* spp. are highest during spring and decline markedly by fall (Johnson and Brinkhurst 1971; Cederwall 1977; Johnson 1988). Gardner et al. (1985) found that *P. hoyi* use up their stored lipid (mainly triglycerides) between July and December as a result of decreasing food supply. Similarily, the burrowing amphipod *C. volutator* grows rapidly by feeding on benthic diatoms in summer (Stuart et al. 1985), whereas at other times of the year the ingested detritus in the sediment was just sufficient for their survival.

Comparative Ingestion Rates

The only other direct measure of ingestion by *Pontoporeia* spp. is that of Elmgren et al. (1986), who estimated that 8-mm *Pontoporeia affinis* from the Baltic produce about 3.2 mm^3 fecal pellets·d^{-1} at 7°C. If the density of the fecal pellets is similar to that in Lake Ontario (0.516 mg·mm^{-3}), then the ingestion rate in the Baltic would be 1.6 mg dry sediment·d^{-1}. In Lake Ontario, an 8-mm amphipod had a calculated ingestion rate of only 0.92 mg·d^{-1} at 7°C (equation 5).

Other estimates of the detrital food requirements of *Pontoporeia* spp. are indirect estimates from information on their assimilation. Johnson and Brinkhurst (1971) estimated assimilation by the bottom fauna in Lake Ontario beyond 100 m (FWPCA samples) to be 0.087 kcal·m^{-2}·d^{-1}. If the proportion assimilated by the *P. hoyi* present is the same ratio as their production (0.025/0.037 kcal·m^{-2}·d^{-1}), then assimilation by *P. hoyi* would amount to 8.9 mg organics·m^{-2}·d^{-1}, assuming the average caloric value of *P. hoyi* to be 6.61 kcal·g ash-free dry weight $(AFDW)^{-1}$ (Johnson and Brinkhurst 1971). With no published assimilation efficiencies (AE) for *Pontoporeia* spp. available, the required ingestion rate of sediment for this amount of assimilation in the middle of Lake Ontario could range between 59 mg organics·m^{-2}·d^{-1} (15% AE, Hargrave 1970) to 14 mg·m^{-2}·d^{-1} (65% AE, Hawkins 1985), as compared with an average of 57 mg·m^{-2}·d^{-1} ingested at the midlake station 41 (125 m, Table 2). Similarily, Johnson and Brinkhurst (1971) calculated assimilation by the crustaceans (biomass = 4.42 g AFDW·d^{-1}) in the eastern basin of Lake Ontario averaged 141.1 kcal·m^{-2}·yr^{-1}. As this biomass was 96% *P. hoyi*, the species' assimilation would be about 56 mg organic matter (AFDW)·d^{-1}. The required ingestion to account for this assimilation would range between 374 (AE 15%) and 86 mg·m^{-2}·d^{-1} (AE 65%). The average OMI of *P. hoyi* at station 81 in the eastern basin of Lake Ontario was 159 mg·m^{-2}·d^{-1} (Table 2). Although these calculations suggest the assimilation efficiency of *P. hoyi* to be near 15%, the AE for *P. hoyi* in Lake Ontario (R. Dermott, unpubl. measurements) can be as high as 65% using dual-labelled algae (Cammen 1977) mixed into sediments as a food source.

Gardner et al. (1985) estimated that the amount of assimilated organic matter required to support the *P. hoyi* production in Lake Michigan was 5.8–11 g organic detritus·m^{-2}·yr^{-1}. This was estimated to be between 11 and 23% of the estimated organic matter settling in Lake Michigan. These ratios are higher than the yearly averages at the Lake Ontario stations during 1981 (4.8–8.8%, Table 2). However, these ratios were similar to the ratio of organic matter ingested to the monthly organic matter trapped as sediment during the early summer (10–24%).

Flint (1986) estimated that the *P. hoyi* population in Lake Ontario requires 24.4 g C·m^{-2}·yr^{-1} as food. Using the average carbon content (38%) of the Lake Ontario sedimented organic matter (Rosa 1985), this would be 64 g organic matter·m^{-2}·yr^{-1}. This high ingestion rate is quite adequate for the more productive eastern basin of Lake Ontario, for which Flint (1986) estimated the population energy requirements using data from Johnson and Brinkhurst (1971). A lakewide estimate of the organic matter consumed by the *P. hoyi* populations in 1981 and 1982 would have been 18.6 and 20.7 g organic matter·m^{-2}·yr^{-1} respectively, assuming the same lakewide population abundances as used to calculate the area-weighted *P. hoyi* production in Lake Ontario (Johannsson et al. 1985).

Marzolf (1965a) stated that until the energy transfer involved in the feeding of *Pontoporeia* spp. is available, the precise role of *Pontoporeia* in the Great Lakes could only be speculative. Its predominance in the benthic fauna of the Great Lakes, and other large holarctic lakes, makes its role in the trophic structure of the lakes vital. The ratios of *P. hoyi* ingestion with the estimates of settling detritus indicate that the amphipods consume a sizable percentage of the organic matter entering the profundal zone of these lakes. The changes in feeding frequency and seasonal lipid levels (Gardner et al. 1985) imply that *Pontoporeia* is adapted to seasonally limited food, but rapidly assimilates newly settled detritus when available. These cycles of

feeding and assimilation have implications into understanding the contaminant dynamics of the species, which must take into consideration seasons during which there is a high incidence of nonfeeding amphipods. The relative importance of the actual components in the diet of this amphipod (bacteria, diatoms, or detrital remains) has yet to be determined.

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Predictability of Change in Shoreline Vegetation in a Hydroelectric Reservoir, Northern Sweden

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We asked whether we could predict the responses of vegetation to specified perturbations acting on a known initial state using 10 yr of vegetation data and precise water level records from the Gardiken Reservoir on the Ume River in Sweden; this has a restricted flora and one obvious controlling factor: water level. Abundance and species richness were strongly correlated for both vascular and nonvascular plants (bryophytes and lichens). Duration of flooding was the most important variable controlling those independent variables chosen for study. The change from year t to $t + 1$ could be roughly predicted for community attributes such as richness and cover ($R^2 > 0.33$) but not for species composition ($R^2 < 0.04$). The initial (preceding-year) state of the system and the duration of flooding (also in the preceding year) were always the two most important independent variables. The major conclusions were that (1) even in this "simple" system with presumably one major control variable, our best regression equation accounted for only 41% of the variation, (2) community properties were more predictable than species composition, and (3) the similarity of the species pool, the lack of coupling from competitive interactions, and the high degree of immaturity may have reduced predictability of species composition.

Les auteurs se sont interrogés sur la possibilité de prévoir les réactions de la végétation à certaines perturbations agissant sur un état initial connu. Ils ont utilisé des données sur la végétation et des enregistrements précis des niveaux d'eau portant sur 10 années. L'étude a porté sur le réservoir Gardiken de la rivière Ume (Suède) dont la flore est restreinte et où le niveau de l'eau a des effets certains. L'abondance et la diversité des espèces présentaient une forte corrélation tant chez les plantes vasculaires que non vasculaires (bryophytes et lichens). La durée de submersion était la plus importante variable régissant les variables indépendantes choisies pour l'étude. Le passage de l'année t à $t+1$ pouvait être prévu, de façon générale, pour certains attributs, telles la richesse et la couverture ($R^2 > 0{,}33$), mais non pour la composition en espèces ($R^2 < 0{,}04$). L'état initial (année précédente) du système et la durée de la submersion (l'année précédente) constituaient toujours les deux variables indépendantes les plus importantes. Les principales conclusions de l'étude sont : 1) même dans ce système « simple » à probablement une seule grande variable déterminante, la meilleure équation de régression n'a pu expliquer que 41 % de la variation; 2) les propriétés de la communauté étaient plus prévisibles que la composition en espèces; 3) la similitude du pool spécifique, l'absence de liens dus à des interactions de compétition et le degré élevé d'immaturité peuvent avoir réduit la prédictabilité de la composition des espèces.

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One major objective of community ecology is to identify the factors structuring communities and to discern whether recurring patterns of community structure exist (e.g. Peters 1980; Wiens 1984; Chesson and Case 1986). Another objective, possibly more important, is to accurately predict future states of communities given a starting state and specified perturbation (Holling 1986; Keddy 1989). Examples of the latter approach include predictions of effects of fire on vegetation (Noble and Slatyer 1977, 1980; Cattelino et al. 1979; Kessel and Potter 1980), effects of water level changes in wetlands (van der Valk 1981; Keddy and Reznicek 1986) and floodplain forests (Franz and Bazzaz 1977), and effects of grazing (Grime 1980; Sinclair and Fryxell 1985). In this study we assessed the possibilities of predicting the short-term (<1 yr) response of a shoreline community to fluctuating water levels.

Reservoirs are ideal systems for such quantitative studies. Their biological diversity is often considerably reduced compared with preimpoundment conditions, and they have one obvious controlling factor (water level) often exhibiting large temporal changes. Furthermore, water level fluctuations are continuously recorded in many reservoirs, offering ideal opportunities for long-term studies. So far, such studies are rare in community ecology (Silvertown 1980; Hynes and Yadav 1985; Goldberg and Turner 1986; Holling 1986; Rose et al. 1986; Kratz et al. 1987).

There are also applied reasons for studying reservoirs. Their growing number has increased the need for management guidelines based on scientific understanding of the factors controlling shoreline plants. Hitherto, most vegetation data available for reservoir management have been qualitative and form the basis

for only very general guidelines. For example, in reservoirs where summer levels are stable and water level fluctuations narrow, shoreline vegetation attains a relatively stable stage within a couple of decades (Kuflikowski 1971; Ekzertsev 1979; Krzyżanek et al. 1986). In contrast, in reservoirs with wide water level fluctuations and unstable water level conditions, shoreline vegetation is highly variable. Years with high water levels often favour amphibious species, while in low-water years, more terrestrial types of vegetation develop (Oliver 1948, 1955; Ekzertsev 1979). The attainment of a more stable state has not been reported from such reservoirs, although many of them have been studied for several years (Tiemeier 1951; Loster 1976; Ekzertsev 1979; Nilsson 1981).

In this study we examined plant – water level relationships using a 10-yr data set from a reservoir shoreline in northern Sweden. This reservoir system constitutes a large-scale natural experiment (sensu Diamond 1986) where water level fluctuations are strictly controlled for hydroelectric purposes, vary greatly from year to year, and are continuously measured. This makes it possible to study in great detail relationships between year-to-year variation in vegetation and environment. We performed the analysis in two steps. First, we assessed the relationships between species richness and abundance and between these two variables and different aspects of the water level regime. Second, our objective was to predict changes in the vegetation from changes in the environment. We especially addressed two questions: (1) Which factor within a given set of water level variables is most highly correlated with changes in shoreline vegetation? (2) Is the plant community modified in a predictable way by specific water level changes?

Study Site

The study was carried out on the shoreline of the Gardiken Reservoir (upstream end 65°40′N, 15°09′E; downstream end 65°29′N, 15°52′E) in the upper Ume River, northern Sweden. This hydroelectric reservoir is 43 km long and covers an area of 84 km². Water level regulation has been in operation since 1961. The high water level is the same through the entire reservoir, but because a series of outlet thresholds in former lakes sets limits on low water levels, the annual drawdown increases downstream to a maximum of 20 m at the dam. The area of shoreline exposed between the high water level and the low water level comprises 56 km² (Fig. 1), the major part of which was formerly shoreline and forests (Wassén 1966). Water level is at its lowest in May, increases rapidly in June, in most years reaches its maximum during July–August, and remains high to October. Thereafter, it is lowered successively during winter, leaving the ice cover on the shoreline until it melts in May–June (Nilsson 1981).

This water regime implies that most of the reservoir shore is barren ground, except for an approximately 1- to 2-m-wide strip (on sheltered shores up to 4 m) of sparse vegetation close to the high water level. The plants growing here exploit the short growing season in early summer before flooding occurs. Thereafter, many of them survive to the next spring as seeds or living basal parts (cf. Gill 1977). However, many individuals also die before reaching maturity (Nilsson 1981). Frequent plant species are *Deschampsia cespitosa*, *Matricaria maritima* ssp. *inodora*, *Poa pratensis* ssp. *alpigena*, *P. annua*, *Ranunculus repens*, *Rumex longifolius*, and the bryophytes *Bryum caespiticium*, *B. pallens*, *Ceratodon purpureus*, *Hypnum lindbergii*, and *Pohlia bulbifera* (nomenclature for vascular plants follows Krok and Almqvist (1984) and for bryophytes follows Koponen et al. (1977)). (Many of these species exhibit a shuttle strategy (During 1979), showing large variation in number from year to year (Nilsson 1981).)

Methods

Sampling Procedures

Our data set consisted of species abundances of vascular plants, bryophytes, and lichens sampled during the period 12–

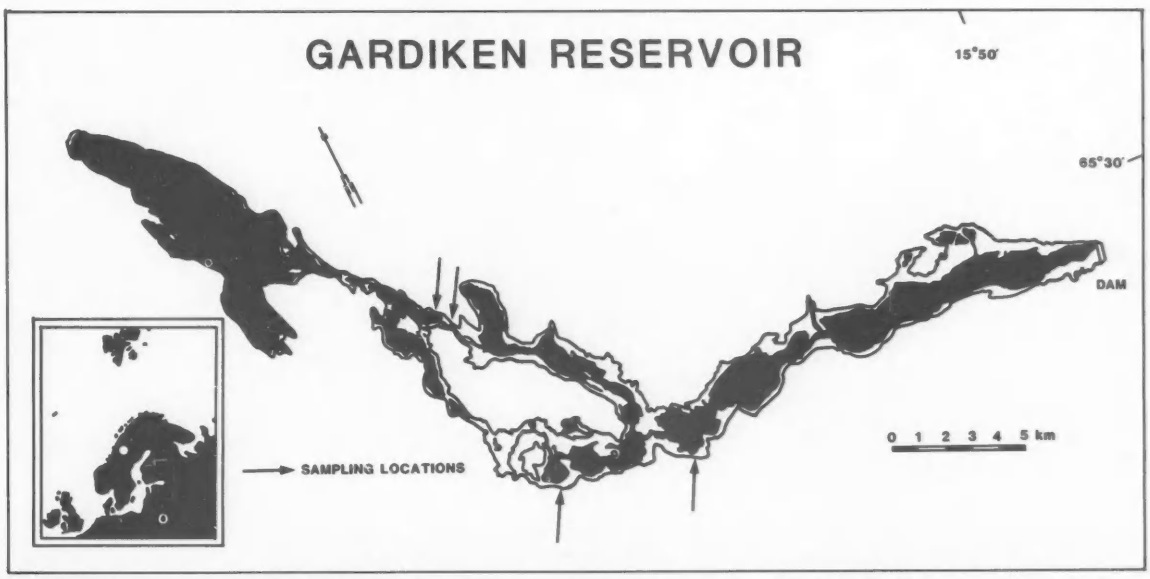

FIG. 1. Location of the study sites in the Gardiken Reservoir, northern Sweden. The reservoir is delimited by its high water level, and the former water system is blackened. The present-day water level fluctuates between these two levels.

19 June each year during 1976–85. Sampling units were a total of forty-eight 1 × 1 m quadrats arranged contiguously along four transects in the middle parts of the reservoir (Fig. 1). Two sites, with a moderate wave exposure, had a coarse gravel substrate and two weakly exposed sites a rather fine-grade gravel uppermost and fine sediments lower down. Close to the high water level there was a distinct scarp between the more or less intact humus cover and the mineral soil. For a more detailed description of the sites, see Nilsson (1981).

The belt transects ran from the high water level down to the lowest occurrences of living plants about 1 m vertically below. At the weakly exposed shore sites, transects were extended about 1 m further vertically because of the greater vertical extent of vegetation at these sites. Because sampling was carried out 10 times for each quadrat the entire data set consisted of $10 \times 48 = 480$ sample units.

Percentage cover (abundance) of the above ground parts of plants was measured on an octave scale (Gauch 1982) using a 1-m² frame, divided into one hundred 1-dm² squares. The elevation at the upper and lower edge of each quadrat was determined using a surveyor's level and a measuring rod. Water level data were given as the daily water level at 7 a.m.

Dependent Variables

We calculated 10 dependent variables: five for vascular plants and five for bryophytes and lichens. Community attributes were described by species richness and total abundance (the sum of all cover values). Temporal variation was described by change in richness and abundance from year t to $t+1$ and by similarity between year t and $t+1$. Following recommendations given by Hajdu (1981) and Legendre and Legendre (1983), we used Kulczynski's (1928) index of similarity. In a comparison of 16 resemblance measures, assessing their power of resolution and linearity, Hajdu (1981) considered this and two other indices to have "the best chance of being successful in most relevé sets." It has a balanced sensitivity, being influenced to the same degree by the common as by the differential species, and it is adapted to transformed abundance data of the type we had. The coefficient is computed as follows:

$$(1) \quad S(x_1, x_2) = \tfrac{1}{2}(W/A + W/B)$$

where A is the sum of species abundances in sample x_1, B is the corresponding value for sample x_2, and W is the sum of the minimum abundance values for each species obtained when comparing both samples. For example, if sample x_1 consists of five species a–e and sample x_2 consists of three species a–c, each with a cover value of 2.0, then $A = 2 + 2 + 2 + 2 + 2 = 10$, $B = 2 + 2 + 2 = 6$, $W = 2 + 2 + 2 = 6$, and $S = 0.8$.

Some quadrats were devoid of vegetation. By definition, a comparison between a quadrat with and without vegetation, or between two quadrats without vegetation, resulted in an undefined (missing) similarity value. A similarity of 0 occurred only when two quadrats had completely different floras.

The final data set consisted of four variables with 48 (quadrats) × 10 (yr) = 480 values each and six variables with 48 × 9 (pairs of yr) = 432 values each. Since we compared year t with $t+1$, we excluded the first year's data of species richness and abundance so that there were 9 yr for each variable in each quadrat.

Independent Variables

There are no data on the length of the growing season on the reservoir shoreline. However, to judge from data from the nearest climatic station (Hemavan, approximately 40 km north) the average growing season on land starts in May and ends in September. Therefore, we calculated independent variables for the period 1 May – 30 September.

Seven water level variables were calculated. These were divided into two subsets: one describing magnitude of flooding (duration of flooding, maximum water depth, longest flood period, longest dry period) and the other describing variation of flooding (date of first flood, date of last flood, number of floods). A quadrat was considered flooded when its midlevel was flooded and dry when the midlevel was above the waterline.

As for the dependent variables, each of the water level variables was determined for each of 9 yr. However, since the analyses of vegetation were always made before the seasonal flooding period, the vegetation studied was compared with the water level fluctuations in the preceding year.

The descriptors of the biota during the previous year were also introduced as independent variables. In total, there were four such variables, i.e. species richness and total abundance for vascular plants and the same for bryophytes and lichens. For the change in species composition, measured by similarity, the initial (preceding-year) state of the system is considered by the formula itself.

TABLE 1. Correlation matrix among the seven water level variables. Correlation coefficients within the two subsets have been underlined. $r > 0.17$; $P < 0.001$; $n = 329$.

	Magnitude				Variation	
	Duration of flooding	Maximum depth of flooding	Longest flooded period	Longest dry period	Date of first flood	Date of last flood
Magnitude						
Duration of flooding	1.00					
Maximum depth of flooding	0.71	1.00				
Longest flooded period	0.97	0.71	1.00			
Longest dry period	−0.68	−0.42	−0.61	1.00		
Variation						
Date of first flood	−0.66	−0.40	−0.60	0.99	1.00	
Date of last flood	0.51	0.50	0.44	0.01	0.05	1.00
Number of floods	−0.20	−0.26	−0.37	−0.07	−0.07	0.07

TABLE 2. Correlation matrix among the variables describing vegetational pattern. $r > 0.17$; $P < 0.001$; $n = 329$.

	Vascular plants		Bryophytes and lichens	
	Abundance	Species richness	Abundance	Species richness
Vascular plants				
Abundance	1.00			
Species richness	0.85	1.00		
Bryophytes and lichens				
Abundance	0.52	0.55	1.00	
Species richness	0.50	0.59	0.86	1.00

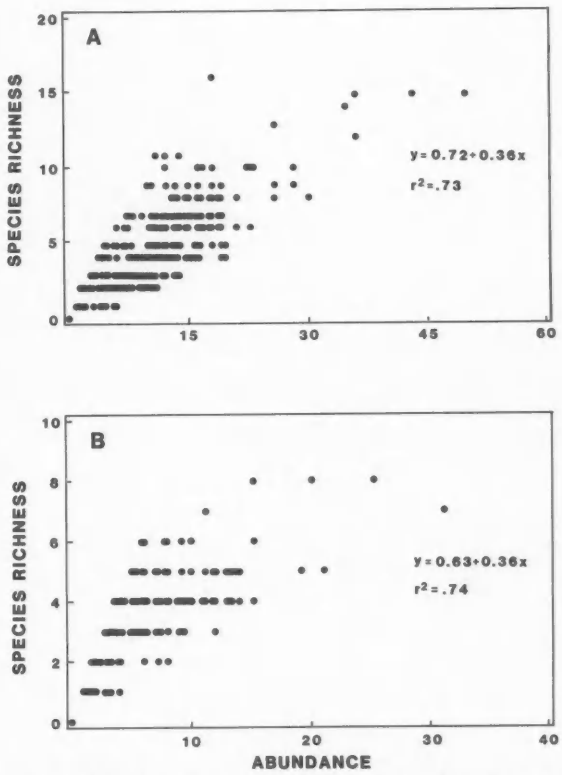

FIG. 2. Relationship between abundance and species richness for (A) vascular plants and (B) bryophytes and lichens. Data for the entire 9-yr period are combined, but years without floods during the growing season were omitted. See text for full explanation of abundance scores. Note different scales.

Data Analysis

Relationships among variables were assessed by means of a Pearson correlation coefficient. To determine the influence of different hydrological factors on vegetation change, we performed a step-wise multiple regression analysis using the SPSS package. Missing values among the timing and similarity variables were deleted listwise, implying that in all analyses, all cases involving unflooded years or unvegetated quadrats were omitted.

Results

Water Level Variables

The four water level variables describing the magnitude of flooding were all strongly correlated ($r = \pm 0.42$–0.97; $P < 0.001$) whereas those describing variation of flooding were uncorrelated ($r = \pm 0.05$–0.07; $P > 0.05$) (Table 1). Therefore, we chose duration of flooding, since it is one of the simplest to measure. The final list of hydrological variables consisted of four variables: duration of flooding, date of first flood, date of last flood, and number of floods.

Patterns of the System

Abundance and species richness were highly correlated ($P < 0.001$), both for vascular plants ($r = 0.85$) and for bryophytes and lichens ($r = 0.86$) (Table 2; Fig. 2). The correlation coefficients were high even for correlations between vascular plant vegetation and bryophyte and lichen vegetation ($r = 0.50$–0.59).

Richness of vascular plants ranged from 0 to 16 species · m^{-2} ($\bar{x} = 4.1$) and of bryophytes and lichens from 0 to 8 species · m^{-2} ($\bar{x} = 1.8$) (Fig. 2). The abundance score for vascular plants was <20 in most quadrats. An abundance score of 20 with five species present (Fig. 2) implies a mean score of 4 on the octave scale, corresponding to a percentage cover between 2 and 4 (Gauch 1982). Assuming no overlap between species, vegetation cover in the example then totalled 10–20%. The vegetation of bryophytes and lichens was even sparser than that of vascular plants (Fig. 2).

Duration of flooding was the most important factor associated with vegetation pattern whereas timing of floods was the least important (Table 3). All four variables showed some relationship to vegetation pattern even if some of the correlation coefficients were low (Table 3).

We also examined whether overall changes in species composition differed between the weakly exposed and the moderately exposed shore types. Differences in exposure levels were relatively unimportant in this context (Fig. 3). Similarity patterns were almost the same for vascular plants and bryophytes and lichens, with comparatively small changes dominating and large changes occurring infrequently.

Changes of the System

The initial (preceding-year) state of the system was the most important variable for predicting the magnitude and direction of changes in abundance and richness (Table 4). It was entered first in the equation in three out of four cases (Fig. 4). Duration of flooding was the most important water level variable associated with change in shoreline vegetation. It was significantly correlated with abundance and species richness of both the vascular plant vegetation and the bryophyte and lichen vegetation (Fig. 5). On average, at intermediate levels of flooding (around 40–60 d · yr^{-1}; Table 5), there was no change in either abundance or species richness. However, at shorter durations of flooding the values of both these variables increased whereas at longer durations they decreased.

The only independent variables which were positively correlated with the value of a biological variable were the date of last flooding and the number of floods (Table 4). Table 4 also shows that the changes in species richness and abundance in shoreline vegetation were difficult to predict ($R^2 < 0.41$). The

TABLE 3. Correlation matrix among the variables describing vegetational pattern and water level variables. *P <0.05; **P <0.01; ***P <0.001; n = 329.

	Duration of flooding	Date of first flood	Date of last flood	Number of floods
Vascular plants				
Abundance	−0.14**	−0.04	−0.05	0.14**
Species richness	−0.26***	0.03	−0.16**	0.17***
Bryophytes and lichens				
Abundance	−0.28***	0.07	−0.10*	0.13**
Species richness	−0.30***	0.11*	−0.12*	0.13**

TABLE 4. Results of the step-wise multiple regression analyses. The independent variables having a significant positive or negative influence on vegetational dynamics are indicated by their respective sign. Figure 5 shows the order of entry of variables and the change in R^2 associated with each; the state of the system and the duration of flooding, both in the preceding year, were always most important. Parentheses denote that change in composition cannot be related to composition in the preceding year, since this variable does not take a numeric value.

	Duration of flooding	Date of first flood	Date of last flood	Number of floods	Initial state of system	R^2
Vascular plants						
Change in abundance	−	−	+		−	0.33
Change in richness	−	−	+		−	0.37
Change in composition				+	( )	0.02
Bryophytes and lichens						
Change in abundance	−	−	+		−	0.41
Change in richness	−				−	0.39
Change in composition	−				( )	0.04

TABLE 5. Relationships between change in communities and duration of flooding.

	Equation	P	R^2	Duration of flooding for no change (d)
Vascular plants				
Change in abundance	$y = 2.91 - 0.07x$	<0.001	0.19	41.6
Change in species richness	$y = 1.18 - 0.03x$	<0.001	0.14	39.3
Bryophytes and lichens				
Change in abundance	$y = 3.26 - 0.06x$	<0.001	0.17	54.3
Change in species richness	$y = 1.19 - 0.02x$	<0.001	0.12	59.5

changes in vegetation composition, expressed by the values of similarity, were unpredictable in terms of hydrological factors (R^2< 0.04), although the number of floods and the duration of flooding explained significant (P < 0.05) portions of the variation in similarity for vascular plants and bryophytes and lichens, respectively.

Discussion

State of the System

The results demonstrate a sparse vegetation with a clear positive relationship between species richness and abundance for both vascular plants and bryophytes and lichens. Grime (1973, 1979) postulated that such relationships should occur only in highly stressed and disturbed habitats (see also Connell 1978; Huston 1979). Our results are consistent with this suggestion, since flooding is known to impose stress on emergent vegetation (Jackson and Drew 1984). Richness is known to be related to biomass in other wetlands (e.g. Wheeler and Giller 1982; Wisheu 1987; Day et al. 1988).

There are at least three different explanations of the observed correlations: (1) long floods kill emergents, therefore reducing species richness and abundance; a long flood means that fewer floods can occur per year; therefore, the number of floods is positively correlated with species richness and abundance; (2) many short floods keep the substrate wet, increasing productivity and the number of species; and (3) there was some other variable x, not measured, which controls species richness.

Site-Specific Management Recommendations

The vegetation was most stable when there was around 40–60 d of flooding during the growing season (Fig. 5; Table 5). This suggests that if more species and a more abundant vegetation are the goal for management, flooding should be kept

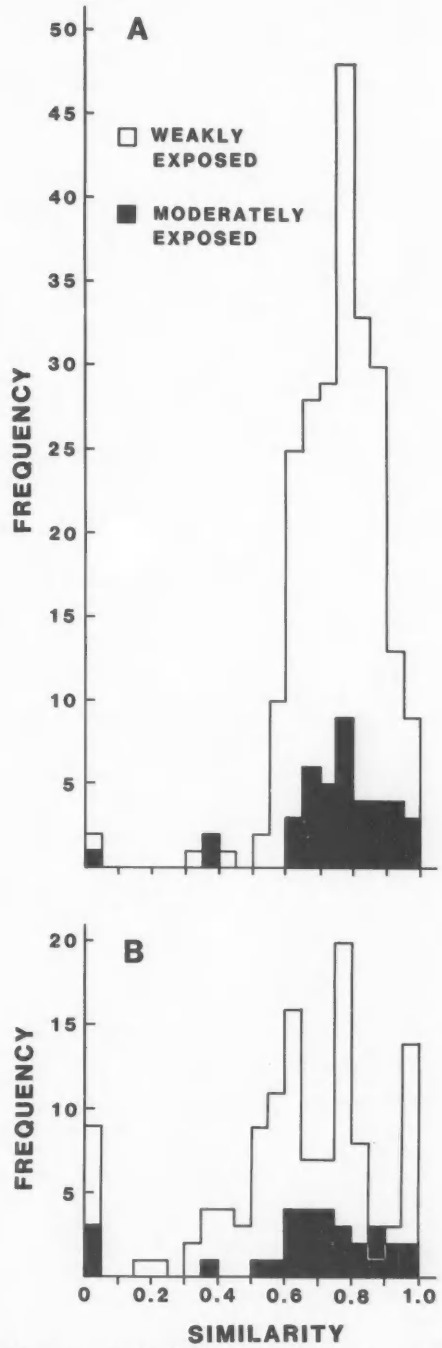

FIG. 3. Frequency distribution of similarity between year t and $t + 1$ for moderately exposed and weakly exposed shores. Data are from a 10-yr period, i.e. nine pairs of successive years. (A) Vascular plants; (B) bryophytes and lichens.

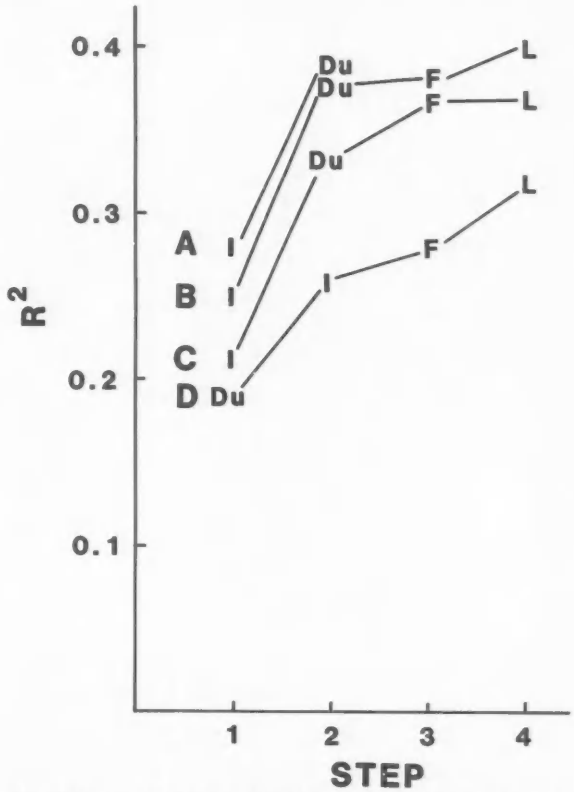

FIG. 4. Entry of variables and the change in R^2 in the step-wise multiple regression analyses (see also Table 5). A, change in richness of bryophytes and lichens; B, change in abundance of bryophytes and lichens; C, change in richness of vascular plants; D, change in abundance of vascular plants; I, initial state of system; Du, duration of flooding; F, date of first flood; L, date of last flood.

shorter than 40–60 d, at least during the growing season. This should, in general, be a goal for management, since shoreline vegetation anchors the substrate and increases the productivity of the shoreline habitat. In contrast, if flooding longer than 40–60 d occurs, vegetation cover will decline even more.

Predicting Vegetation Change

We chose a system where a single environmental factor could be responsible for much of the vegetation change. Despite having the water level fluctuations recorded with great accuracy, and despite long-term records of vegetation, we could not predict more than 41% of this change. One may argue that the addition of another overlooked factor may considerably increase the degree of explanation. However, it seems unlikely in this strongly regulated reservoir that any factor other than the water level regime (primarily the magnitude of flooding) could be the major environmental determinant of the temporal variation in vegetation. Water depth is also generally considered to be the major factor controlling shoreline vegetation within a lake (Hutchinson 1975; Spence 1982; Duarte et al. 1986) and within shoreline wetlands (Auclair et al. 1976; van der Valk 1981; Lieffers 1984; Day et al. 1988). Rather than assigning the unexplained variation simply to "stochastic events," we suggest that several other minor factors may have been important when combined. A list of such potential variables may include both abiotic factors (weather during the growing season, rainfall,

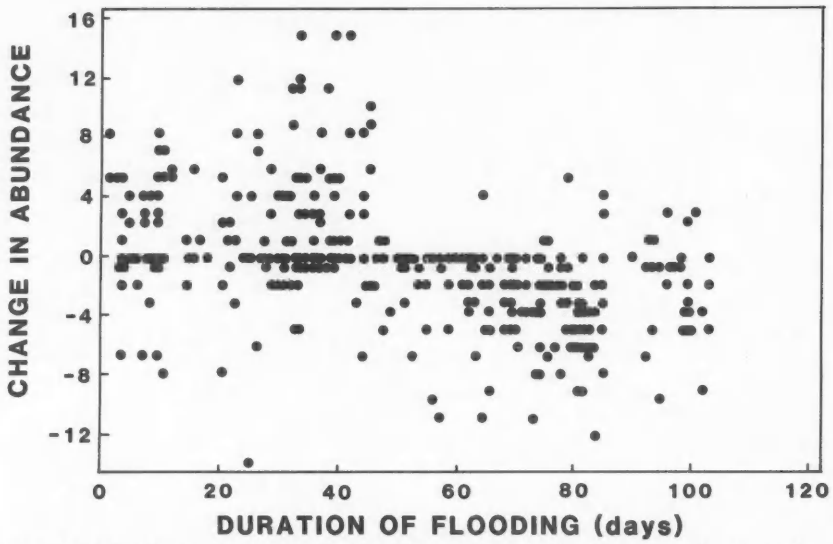

FIG. 5. Relationship between the duration of flooding and change in abundance of vascular plants. Data for 9 yr are combined, but years without floods during the growing season were omitted. For further information see Table 5. See text for full explanation of abundance scores.

storms), biotic factors (germination requirements, pathogens, seed bank, seed dispersal, winter mortality), and possibly sampling errors.

Although differences in exposure between quadrats did not seem to affect year-to-year variability (Fig. 3), one might argue that such differences, for example in nutrient availability, soil organic matter, etc., might influence variation patterns (Walker and Wehrhahn 1971; Hutchinson 1975; Auclair et al. 1976; Lieffers 1984; Day et al. 1988). Therefore, restricting the permanent quadrats to very similar habitats might have enhanced predictability — but at the cost of loss of generality.

The changes in species composition, as opposed to overall community attributes like cover and richness, were unpredictable. This might have been a consequence of the similar kinds of species involved, most being herbaceous perennials with a ruderal strategy. Out of 92 species, there were only two annuals, and these were uncommon. This is a major reason why spring conditions for germination were considered to be relatively unimportant in controlling species richness. Conditions affecting seed germination might otherwise have been of crucial importance in this respect (Hall et al. 1946; Grubb 1977; Keddy et al. 1989). One might also argue that the use of another coefficient of similarity would have given other results. However, should changes in species composition have been easily predictable, patterns should emerge irrespective of the coefficient used.

We did not find that the simple system investigated was easily predictable. In fact, it is likely that the changes in vegetation would have been easier to predict had the mixture of species been more complex so that different functional groups (sensu Day et al. 1988) occurred. It is usually assumed that it is easiest to develop predictive models for very simple systems, but if ecologically similar species occur in such "simple" systems, then future states may depend on minor differences in morphology, physiology, or life history. Choosing sites with mixtures of very different species may lead to more predictable changes in composition over time.

A further difficulty in predicting changes in species composition may have been the relative independence of each species from all others. The sparseness of the vegetation suggests that competition was relatively unimportant. According to Fig. 2, and following Grime (1979), we also suggest that stress and/or disturbance are the major controlling factors. There was little evidence of vegetation closure. Experimental studies have shown that sites with low cover or standing crop have relatively weak interspecific competition (Wilson and Keddy 1986a) and could have species with low competitive abilities (Wilson and Keddy 1986b). Under these conditions, a major increase or decrease in one species might have relatively little effect upon cooccurring species. If the species were "uncoupled" or "independent" in this way, year-to-year similarity, and the predictability of the vegetation, would be expected to be very low.

In conclusion, the state of the system in the preceding year was the most important variable for predicting change in shoreline vegetation. The magnitude (duration) of flooding (also in the preceding year) was the most important water- level factor. It reduced significantly both species richness and abundance. In contrast, the variation of flooding was less important. Given the initial state of the system and the water level fluctuations, we could predict 33–41% of the changes in species richness and abundance in the vascular plant vegetation and in the vegetation of bryophytes and lichens. On the other hand, the changes in species composition were unpredictable. This was probably due to two factors: (1) most species were functionally similar and (2) competition was insignificant. Systems with a more complex array of species, and more coupling of populations, may have a more predictable behavior.

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Response of Headwater Lakes to Varying Atmospheric Deposition in North-Central Ontario, 1979–85

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Between 1976 and 1985, loadings of SO_4^{2-} to the Algoma district (north-central Ontario) varied from a low of 47 (1980) to a high of 84 meq·m^{-2} (1978) and was low in years of low annual precipitation. The mean and median lake concentrations of H^+ and SO_4^{2-} in 54 lakes declined between 1979 and 1982 following the period of lowest annual deposition and declined further between 1982 and 1985. Overall, mean lake pH increased 0.35 unit between 1979 and 1982 and an additional 0.07 unit over the next 3 yr. Lake concentrations in the Turkey Lakes watershed exhibited a similar trend. Two lakes without fish in 1979 and with pH's < 5.5 developed white sucker (*Catostomus commersoni*) populations by 1986 with ages indicating that survival began after 1980. This apparent invasion from downstream populations probably occurred when lake pH's neared 5.5. Although a direct link has not been established, these lakes appear to be extremely responsive to changes in atmospheric deposition. The "recovery" of water quality clearly extends beyond that locally documented at Sudbury, Ontario, yet it remains to be determined to what degree the responses relate to differences in continental deposition and/or responses within the watershed.

De 1976 à 1985, la charge de SO_4^{-2} du district d'Algoma (centre-nord de l'Ontario) est passée d'un minimum de 47 (1980) à un maximum de 84 méq·m^{-2} (1978). La charge était peu élevée les années de faibles précipitations. Les concentrations moyenne et médiane de H^+ et de SO_4^{-2} des eaux de 54 lacs ont diminué de 1979 à 1982, suite à la période de plus faibles dépôts annuels, et diminué encore plus de 1982 à 1985. De façon globale, le pH moyen des lacs s'est accru de 0,35 unité, de 1979 à 1982, et d'un autre 0,07 unité au cours des trois années suivantes. Les concentrations dans les eaux des bassins versants des lacs Turkey ont présenté une allure semblable. Deux lacs ne contenant aucun poisson en 1979, année où le pH était inférieur à 5,5, présentaient des populations de meunier noir (*Catostomus commersoni*) en 1986. Les âges des poissons montraient que ceux-ci avaient commencé à y survivre après 1980. Cette invasion de populations situées en aval s'est probablement produite lorsque le pH du lac s'est approché de la valeur de 5,5. Bien qu'un lien direct n'ait pas été établi, ces lacs semblent extrêmement sensibles aux variations des dépôts atmosphériques. Le « rétablissement » de la qualité de l'eau déborde nettement le cas étudié localement à Sudbury (Ontario), mais il reste à déterminer dans quelle mesure ces réactions traduisent des écarts des dépôts continentaux et/ou des réactions originant au sein même du bassin versant.

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Beggs and Gunn (1986), Keller et al. (1986), Dillon et al. (1986), Hutchinson and Havas (1986), and Keller and Pitblado (1986) have all demonstrated that water quality and, to a lesser extent, biota in lakes of the highly impacted Sudbury area of Ontario have recently changed towards a more "normal" condition. All authors attributed this change to decreased local emission (and therefore local deposition) of sulphur oxides from the major smelting operations of the area, achieved by both emission control and reduced production. These observations in the Sudbury area support the contention that lake acidification is chemically reversible when deposition is reduced as reported in Nova Scotia (Thompson 1986), Sweden (Forsberg et al. 1985; Morling et al. 1985), and in the experimental RAIN Project in Norway (Wright et al. 1986).

It has been unclear whether the "recovery" of water quality and biota in Sudbury area lakes extends beyond the locale reported. Scheider et al. (1981) have shown that deposition of H^+ and SO_4^{2-} at Muskoka–Haliburton (approximately 200 km southeast of Sudbury and with no significant local sources) was unaffected by the complete shutdown of the dominating emitter at Sudbury. Therefore, we examined a lake data base in the Algoma region of Ontario for changes in chemistry and fisheries that occurred between 1979 and 1985.

Study Area

The Algoma region is a pristine location approximately 200 km from Sudbury, but in a westerly (and therefore in a generally

TABLE 1. Comparison of the size distribution of lakes within the study region (Cox 1978) with our sample of headwater lakes.

Lake surface area (ha)	Cox (1978)		This study	
	Number	%	Number	%
>1000	3	0.02	0	0
999–100	60	0.3	2	4
99–10	784	4.0	32	59
9.9–1	16 983	87.0	21	39
<1	1 691	8.7	0	0

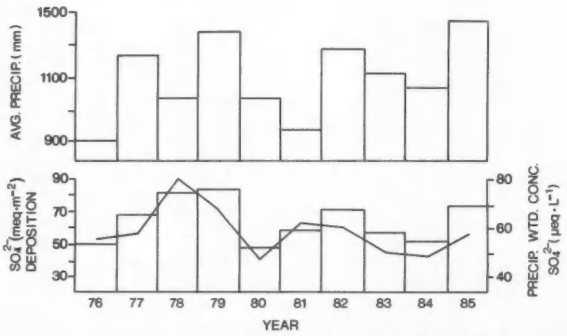

FIG. 1. Average annual precipitation and SO_4^{2-} deposition to the Algoma region of Ontario, 1979–85. The solid line in the bottom panel is the precipitation-weighted concentration of SO_4^{2-}.

upwind) direction. Fifty-four headwater lakes were identified from 1 : 50 000 topographic maps. All lakes lie on the Canadian Shield in the highland area east of Lake Superior. Bedrock is composed of either greenstone that exists in a discontinuous arcuate belt or granitic silicates and is overlain by glacial deposits of variable thickness. Only those lakes not perturbed by logging, mining, or extensive cottage development and not dystrophic were sampled.

Because the lakes were all headwater systems, lake size was biased towards small lakes. Comparison of our lake sizes with those of Cox (1978) measured in the appropriate watersheds shows that our selection process created a bias away from very small (<1 ha) and large (>100 ha) lakes (see Table 1).

Methods

Lakes were sampled after fall overturn in 1979, 1982, and 1985. Sampling procedures were described by Kelso et al. (1982) and 1979 data were analyzed by Kelso et al. (1986a) and Jeffries et al. 1986b. In all cases, pH and acid-neutralizing capacity (ANC) (Gran titration technique) were determined within 24 h on samples kept cold and in the dark.

Identical precautions and calibration procedures (even the same meters) were employed on all three occasions. Other chemical constituents were determined using standard methodology (Environment Canada 1979) either at the Canada Centre for Inland Waters, Burlington (1979), or the Great Lakes Forestry Centre, Sault Ste. Marie (1982 and 1985). Both laboratories participated routinely in an intercomparison program (Long Range Transport of Atmospheric Pollutants Interlaboratory Comparison) under the auspices of the Quality Assurance and Methods Section, Analytical Methods Division, National Water Research Institute, Burlington, Ontario. The data were

TABLE 2. Mean, median, and range for pH and the most important ionic constituents (μeq·L^{-1}) in 54 lakes repetitively sampled in the Algoma district of Ontario, 1979, 1982, and 1985.

Parameter	Date	*n*	Mean	Median	Range
pH	1979	54	6.23	6.35	4.60–7.10
	1982	53	6.58	6.64	5.16–7.82
	1985	54	6.65	6.65	5.44–7.90
H^+	1979	54	1.62	0.41	0.08–25.1
	1982	53	0.59	0.23	0.02–6.92
	1985	54	0.44	0.20	0.01–3.63
Ca^{2+}	1979	54	185	151	80–599
	1982	52	186	152	78–571
	1985	54	168	136	71–564
ANC	1979	48	108	79	(−9)–505
	1982	53	123	86	5–486
	1985	54	115	76	13–478
SO_4^{2-}	1979	53	134	133	94–177
	1982	52	118	118	60–161
	1985	51	108	106	50–159

edited using charge balance criteria and any erroneous data were removed. If the suspect ion could not be identified, then the sample was excluded from the analysis that follows.

Between-sample variation (i.e. 1979–1982, 1979–1985, and 1982–1985) was assessed using a paired *t*-test. Regression analyses were performed to determine whether differences fell outside the 95% confidence level, assuming the data were randomly distributed, and to determine relationships between chemical constituents and lake morphometric characteristics. All statistical computations were completed using SPSS (Version 9).

In the Algoma area, precipitation quantities (814–1123 mm·yr^{-1}, average = 935 mm·yr^{-1}) vary substantially due to orographic factors. In order to have a single estimate of annual atmospheric deposition for the area, we calculated a composite value for each year, 1976–85, as the product of a mean precipitation composition and a mean precipitation quantity. Precipitation composition was measured at the Great Lakes Precipitation Network station, 1.0 km from the shore of Lake Superior, and/or in the Turkey Lakes Watershed (TLW) located at higher elevation (Semkin and Jeffries 1985) some 15 km inland. While neither station operated for the entire 1976–85 period, the stations taken together do cover the period. Variation in deposition within the region is primarily related to variation in precipitation quantity, and an average was determined from the mean of precipitation at Sault Ste. Marie Airport and Montreal Falls.

Lakes with pH < 5.5 in 1979 were fished with gill nets in an identical manner in 1979 (seven lakes), 1982 (three lakes), 1985 (one lake), and 1986 (seven lakes). Multifilament gill nets consisted of seven panels each 9.1 m long with 2.8-, 5.1-, 6.4-, 7.6-, 8.9-, 10.2-, or 12.7-cm stretched measure mesh. Catches were adjusted to catch per unit effort (CUE) per 24-h net set. All fish were aged from scales and assigned ages were corroborated by two independent scale readers. Because most fish were young, <4 yr, and most (92%) age assignments were consistent between two persons who aged fish, we assumed that scales adequately reflected age. Also, recapture of four marked fish 3 yr later confirmed the value of scales for aging of fish from at least one lake.

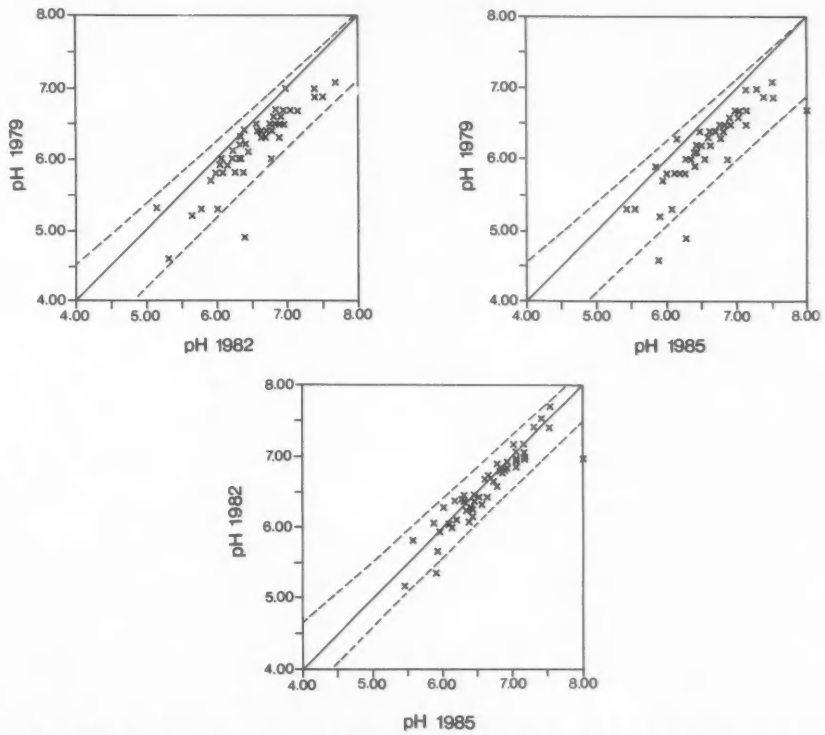

FIG. 2. Scatter plots of pH for three possible year pairings for 54 lakes in north-central Ontario (95% confidence belts are included).

Results

Atmospheric Deposition, 1976–85

Average annual precipitation to the area ranged from a low of 920 mm in 1976 to 1280 mm in 1985 (Fig. 1). The pattern of SO_4^{2-} deposition tends to mimic that of precipitation (Fig. 1). This was expected, given that SO_4^{2-} concentrations tend to be higher in the warmer months (rainfall accounts for approximately 70% of the annual total deposition (Semkin and Jeffries 1985)). The annual precipitation-weighted SO_4^{2-} concentration for the 8-yr period exhibited a small downward trend as apparently did the trend in SO_2 emissions from eastern North America (BACG report, in prep.; Environmental Protection Service 1986; Ontario Research Foundation 1986). Of greater significance to this paper is the low SO_4^{2-} deposition that occurred in 1980 and later apparently resulting from the combined effect of low precipitation quantities and low average SO_4^{2-} concentrations.

Lake Chemical Change, 1979–85

pH was significantly different (two-tailed probability < 0.05) between all combinations of years (Table 2). The greatest increase in pH was between 1979 and 1982. SO_4^{2-} concentrations were significantly different among all year pairings, and Table 2 suggests a somewhat gradual decrease in SO_4^{2-}. ANC was significantly different between 1979 and 1982 (mean difference negative) and between 1982 and 1985 (mean difference positive), but not between 1979 and 1985. In general, ANC appeared higher in 1982 and 1985 but a small decline after 1982 occurred (Table 2). Ca^{2+} was not significantly different between 1979 and 1982, but was different for the other two-year pairings. Ca^{2+} appeared to decline (Table 2) particularly between 1982 and 1985.

Only in 1979 were there any lakes with negative ANC values and pH < 5.0 (Table 2; Fig. 2). Overall, mean lake pH increased 0.35 unit between 1979 and 1982 and an additional 0.07 unit over the next 3 yr. Concommitently, mean SO_4^{2-} decreased 16 and 10 $\mu eq \cdot L^{-1}$, respectively (Table 2; Fig. 3). It is clear from Fig. 2 and 3 that there were few exceptions to the average changes noted above. Only 1 lake of 53 did not increase in pH between 1979 and 1982 and 2 lakes of 54 between 1979 and 1985. The relatively small increase in mean pH between 1982 and 1985 is reflected in the grouping of points around the 1:1 line in Fig. 2. Over 90% of the lakes exhibited decreased SO_4^{2-} for any year pairing (Fig. 3).

The year-to-year changes in chemical composition were also examined using comparable data collected for lakes in the TLW. The TLW is located within the survey region (see Jeffries and Semkin 1982) although none of the members of the four-lake chain within it are included in data analyzed above. Lake concentrations in the TLW (Fig. 4) exhibited similar trends as in the survey data base, i.e. decreasing SO_4^{2-} and Ca^{2+} over the study period, and maximum ANC occurring in the middle of the period. The TLW data also show that the greatest year-to-year differences in concentrations occurred between 1980 and 1982.

Since the rate of chemical response of a lake to an external perturbation is influenced by its physical characteristics, we regressed year-to-year differences of all chemical constituents

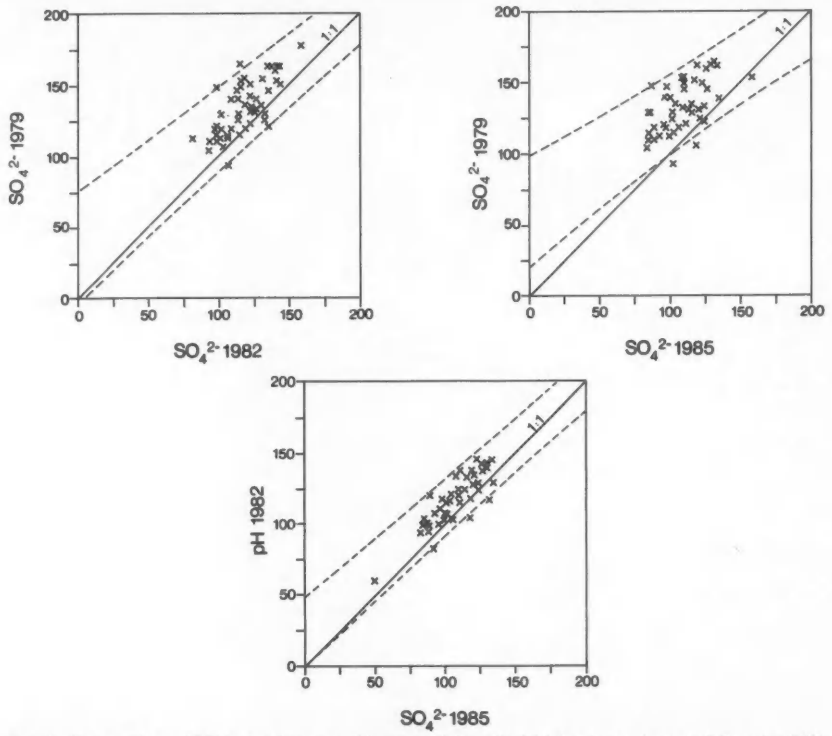

FIG. 3. Scatter plots of SO_4^{2-} for three possible year pairings for 54 lakes in north-central Ontario (95% confidence belts are included).

of the 54 lakes against maximum depth (Z_{max}), drainage basin area (A_d), lake surface areas (A_o), A_d:A_o, and a theoretical flushing rate (flushing rate was estimated by calculating mean depth using the empirical relationship derived by Kelso et al. (1986b) for lakes in this region, multiplying by the known surface area, and dividing by the product of the known drainage basin area and a reasonable mean value of 0.8 $m \cdot yr^{-1}$ for runoff). The year-to-year differences in chemical constituents exhibited few significant relationships with any of the physical parameters (Table 3), presumably due to the rapid rate of water turnover in these lakes (i.e. the flushing rate was almost always much less than the sampling frequency). Only three chemical constituents (pH, Ca^{2+}, and SO_4^{2-}) showed any significant (correlation $p < 0.05$) relationships at all (usually to Z_{max} or flushing rate), and when these occurred, they were characterized by a broad scatter of most of the points with a much smaller number of wide outliers, thus giving the significant regression correlations.

Fish Populations

Only one of seven lakes with a pH < 5.5 (JR-04) supported a fish population in 1979 (Table 4) and only white sucker (*Catostomus commersoni*) were present. In 1986, two lakes in addition to JR-04 contained a population of white sucker. The CUE in lake JR-04 increased almost four times from 1979 to 1986.

One lake, JR-02, supported white sucker in 1982 (Table 5) when two brood years, 1981 and 1980, were captured. The strong 1981 year class was still evident in samples taken in 1985 and 1986. Lake JR-36, another lake in which no fish were found in 1979, also contained white sucker in 1986, the oldest of which were also from the 1981 brood year. Tables 3 and 4 suggest that white sucker may have invaded these lakes at pH 5.0–5.5. Two strong year classes, 1981 (low annual precipitation) and 1984 ("average" annual precipitation), tended to dominate catches in both lakes that had reestablished fish populations.

Discussion

Our data indicate that wet SO_4^{2-} deposition to the Algoma area ranged from 23 to 40 $kg \cdot ha^{-1} \cdot yr^{-1}$ (1976–85, respectively), higher than expected from U.S./Canada (1983). Our estimated deposition values are in reasonable agreement with carefully measured recent data from the TLW (Sirois and Vet 1988). That region of Ontario, on the fringe of the eastern North American high deposition zone, can be expected to experience extreme shifts in deposition due to variations in both meteorological conditions and SO_2 emission rates.

Our data show considerable change (1979–82) in lake chemistry with a general trend to higher pH and lower SO_4^{2-} (1979–85). The linkage of these trends with changing deposition chemistry is not clear cut; however, the most dramatic year-to-year changes (i.e. 1979–82) were contemporaneous with the most dramatic changes in deposition. The headwater lakes in Algoma appear to respond very quickly to variations in pollutant input due to the high precipitation rate and short water renewal times. Our regional data and data from the calibrated watershed suggest that the input and output of SO_4^{2-} remain

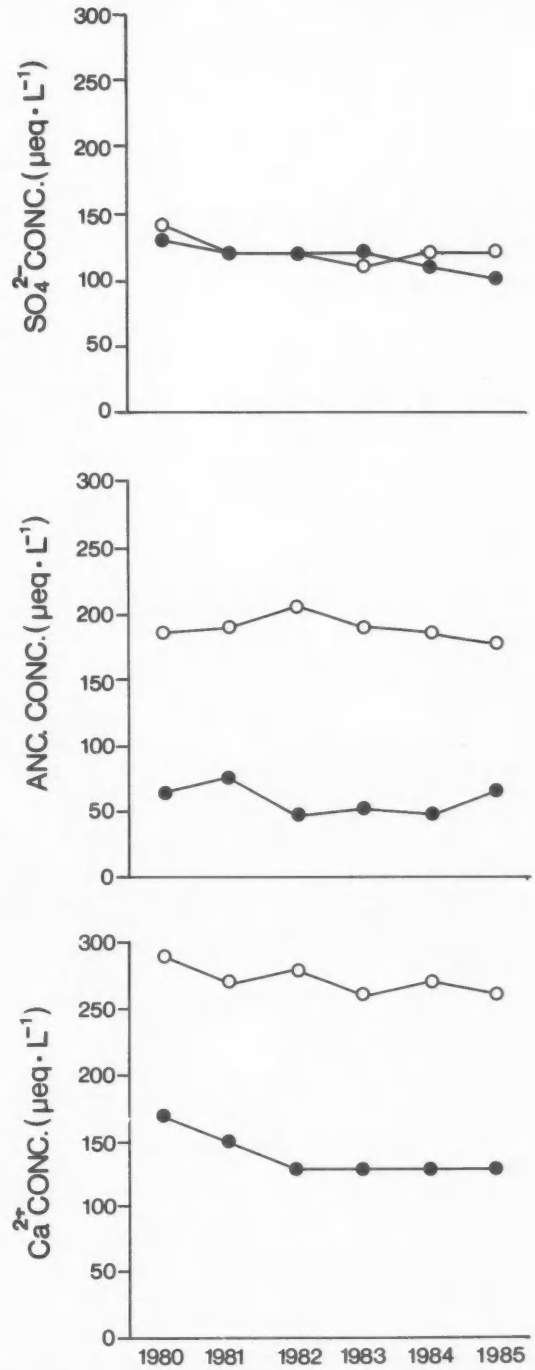

FIG. 4. Scatter plots of SO_4^{2-}, ANC, and Ca^{2+} concentrations in Batchawana Lake South (●) (basin of headwater lake) and Turkey Lake (○) (most downstream lake in the watershed) immediately after fall overturn, 1980–85.

TABLE 3. Mean, median, and range for lake surface area (A_0), drainage basin area (A_d, includes A_0), maximum depth (Z_{max}), A_d:A_0, and theoretical flushing rate (τ) for 54 lakes in the Algoma district of Ontario.

Parameter	Mean	Median	Range
A_0 (ha)	12.8	10.4	3.3–69.0
A_d (ha)	75.2	40.9	8.2–485
Z_{max} (m)	8.9	7.1	2.5–26.0
A_d: A_0	7.1	4.2	1.7–49.5
τ (yr)	1.1	0.75	0.08–5.2

more or less in balance on at least a 3-yr time step. Analysis of the sulphur pools and fluxes in the TLW have shown, first, that there exists a reservoir of SO_4^{2-} in the soils which is large compared with the annual input–output flux and, second, that the annual input of SO_4^{2-} to the lakes in the basin is balanced by output (Jeffries et al. 1986a).

It seems highly probable that a reduction in SO_4^{2-} deposition yielded an increased mean pH for lakes in Algoma — the same conclusion offered by similar Sudbury area studies. Keller and Pitblado (1986) showed that improvements in water quality near Sudbury occurred between 1974 and 1976 and 1981 and 1983, and Keller et al. (1986) suggested that the greatest pH increases and SO_4^{2-} decreases occurred largely between 1977 and 1981. The major changes we observed between 1979 and 1982 are temporally consistent with Sudbury results, suggesting that, at least in part, improvements near Sudbury may be due to altered continental deposition patterns rather than simple reduction in local emissions.

As discussed by Wright (1983) and others, the composition of surface waters respond to elevated SO_4^{2-} concentrations by either decreasing ANC (i.e. "titrating" the water's buffering capacity) or increasing base cations (i.e. through increased soil cation exchange and/or weathering). When SO_4^{2-} decreases, the reverse process can occur. Between 1979 and 1982, decreasing SO_4^{2-} was primarily balanced by increasing ANC that yielded sharply higher pH values. Between 1982 and 1985, further modest SO_4^{2-} declines were matched by lower Ca^{2+}. It is not clear why the lakes responded in different ways during the two intervals, but it may be related to either the response of lakes to different levels in deposition or our ability to detect small changes in aquatic systems.

Changes in surface water Ca^{2+} concentrations in response to changing SO_4^{2-} are usually of lesser importance than changes in ANC (Henriksen 1984; Thompson 1986); however, in Algoma the glacially derived surficial deposits contain a small quantity of easily weathered $CaCO_3$ (Schilts 1981). Hence, it is possible that decreased acidic input in this area results in decreased Ca^{2+} levels in the runoff waters. Our data permit calculation of the ratio of the change in $Ca^{2+} + Mg^{2+}$ to the change in SO_4^{2-} over the study period, the so-called "*F*" factor (Henriksen 1982; Wright 1983). Hence, we have calculated the ratio using changes in median concentrations, since they are probably the best unbiased estimates of the population averages. The data distributions tend to be distorted from normality due to the existence of a small number of lakes having high base cation and ANC concentrations. While not given in Table 2, the measured decrease in median Mg^{2+} concentration from 1979 to 1985 was 6.8 $\mu eq \cdot L^{-1}$, yielding an *F* factor of 0.79. This very high average value for the *F* factor reflects the presence of an easily weathered source of Ca^{2+}, although it should be noted that the geographical distribution of glacial overburden (and therefore the source of Ca^{2+}) is very irregular.

TABLE 4. Morphometric characteristics (1979), pH (1979), and CUE (1979–86) for seven lakes with pH < 5.5.

Lake	Surface area (ha)	Mean depth (m)	1979 pH	1979 CUE	1982 pH	1982 CUE	1985 pH	1986 CUE
JR-02	11.5	8	4.9	0	6.3	2.7	6.3	6.6
JR-04	8.2	4.5	5.2	12.8	5.7	Not fished	5.9	45.3
JR-05	9.8	3.5	4.6	0	5.3	0	5.8	0
JR-08	9.8	2.0	4.8	0	5.4	0	5.5(1986)	0
JR-09	19.7	3.0	5.3	0	6.0	Not fished	6.1	0
JR-34	3.3	7.8	5.3	0	5.2	Not fished	5.4	0
JR-36	6.6	3.5	5.3	0	5.8	Not fished	5.6	9.8

TABLE 5. Brood years of white sucker from two lakes that in 1979 had no fish.

Lake	Collection year	*N*	Brood year 1979	1980	1981	1982	1983	1984	1985
JR-02	1982	16	—	2	14				
	1985	15	—	—	3	1	1	10	
	1986	13	—	—	3	2	1	6	1
JR-36	1986	22	—	—	8	0	3	4	7

Many of the lakes having Ca^{2+} concentrations in the low end of the frequency distribution have *F* factors in the 0.1–0.4 range, more in line with the averages presented by Wright (1983). (Use of mean values, rather than median values, yields higher *F* factor values.)

Our documentation of the recurrence of white sucker in two low-pH lakes does not suggest a colonization and subsequent resumption of recruitment. Scott and Crossman (1973) indicated that white sucker do not reach age of maturity until 3–4 yr in Ontario; therefore, in 1982, no fish capable of reproducing existed in JR-02, and in 1985–86, survivors had barely reached maturity. The stocks evident post-1980 must, therefore, be the result of immigration from downstream. Schindler et al. (1985) and Mills (1984) have shown that white sucker recruitment ceases below pH 5.4; however, we know little of the preference/avoidance reaction of fish over the range of pH values currently found on the Canadian Shield. The existence of fish in headwater lakes may well be ephemeral: lake chemical conditions for reproduction may be marginal (Table 4) in some lakes of this region of Ontario; accessibility can be influenced by beaver; and amount of annual rainfall and environmental conditions can change invoking an avoidance reaction.

We cannot directly link the changes in these north-central Ontario lakes to the changes in atmospheric deposition that have occurred since 1979. However, the "recovery" of water quality in responsive, sensitive aquatic systems of Ontario (including reinvasion of fish) clearly extends beyond that documented near Sudbury and implicates either changing continental deposition patterns or an influence of Sudbury far beyond that currently accepted.

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Chaoborus Predation, Prey Vulnerability, and their Effect in Zooplankton Communities

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We investigated the effect of *Chaoborus* predation on a variety of zooplankton prey through the development, testing, and application of a model of prey vulnerability that predicts prey selection. This model, which is based on the swimming speed of the prey and the strike efficiency of the predator, predicts that *Ceriodaphnia* is 3–4 times more vulnerable to *Chaoborus* predation than is either *Daphnia* or *Diaptomus*. In laboratory feeding experiments, *Ceriodaphnia* was greatly preferred by *Chaoborus* over *Daphnia* and *Diaptomus*; both the order and magnitude of prey selection were accurately predicted by the prey vulnerability model. This especially large impact of *Chaoborus* predation on *Ceriodaphnia*, predicted by the model, was reflected in the community dynamics of a small pond. The seasonal peak of fourth-instar *Chaoborus* in this pond coincided with a sharp decline in *Ceriodaphnia* densities, and the subsequent decline of the predator was immediately followed by a rapid increase of this prey. A field experiment, in which *Chaoborus* densities were manipulated in experimental enclosures in the pond, also demonstrated the substantial impact of this predator on *Ceriodaphnia*. Enclosures with added *Chaoborus* (~1.0 larvae/L) contained 15 times fewer *Ceriodaphnia* and 10 times fewer *Diaptomus* than enclosures that lacked the predator.

On a examiné l'effet de la prédation par *Chaoborus* sur une variété de proies zooplanctoniques tout au cours du développement, de l'essai et de l'application d'un modèle de vulnérabilité des proies visant à prévoir la sélection des proies. Ce modèle, fondé sur la vitesse de nage de la proie et l'efficacité de l'attaque du prédateur, laisse prévoir que *Ceriodaphnia* est de trois à quatre fois plus vulnérable à la prédation par *Chaoborus* que *Daphnia* ou *Diaptomus*. Lors d'essais en laboratoire, *Ceriodaphnia* était largement préférée à *Daphnia* et *Diaptomus* par *Chaoborus*; le modèle a permis de prévoir avec précision l'ordre et l'importance de la sélection des proies. L'effet accentué de la prédation de *Chaoborus* sur *Ceriodaphnia*, prévu par le modèle, est confirmé par la dynamique des communautés dans un petit étang. En effet, on y observe que le pic saisonnier de *Chaoborus* rendu au quatrième stade larvaire coïncide avec une chute abrupte de la densité de *Ceriodaphnia* et que le déclin subséquent de ce prédateur est immédiatement suivi d'un redressement rapide de la population de cette proie. Lors d'un essai sur le terrain, dans lequel la densité de *Chaoborus* était ajustée dans des enceintes expérimentales disposées dans l'étang, on a montré l'effet important de ce prédateur sur *Ceriodaphnia*. Les enceintes qui logeaient des *Chaoborus* (~1,0 larve/L) contenaient quinze fois moins de *Ceriodaphnia* et dix fois moins de *Diaptomus* que les enceintes sans prédateur.

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The effect that predators have on their prey is a key area of investigation in population and community ecology. Predators may not only suppress prey populations, but also, through differential selection, structure entire communities. The influence of visual fish predators on the freshwater plankton is substantial. These planktivores select the largest available prey and create communities dominated by small zooplankton (Brooks and Dodson 1965; Hall et al. 1976; O'Brien 1979). The effect of invertebrate predators on the plankton is not so well documented, but potentially very important. These tactile planktivores, which generally prefer smaller prey (Dodson 1974; Greene 1983), have lower individual feeding rates than fish, but far greater densities, making their overall impact significant.

One of the most widespread, abundant, and important invertebrate planktivores is the larva of the phantom midge *Chaoborus*. These ambush predators lie motionless in the water column (buoyed up by two pairs of air sacs) and strike at zooplankton prey as they swim close enough to be detected by the mechanoreceptors that cover *Chaoborus*' body (Riessen et al. 1984). Prey are captured with prehensile antennae and mandibles and ingested whole. The potential impact of these predators is considerable, as they have been shown to remove up to 20% of certain zooplankton prey populations per day (Lewis 1979; Pastorok 1980a). Field experiments, using enclosures in lakes to manipulate predator densities, have confirmed the great

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effect that *Chaoborus* can have on zooplankton community structure (Smyly 1976; Neill and Peacock 1980; Neill 1981).

Several studies have examined the feeding behavior of *Chaoborus* (Swift and Fedorenko 1975; Swift and Forward 1981; Pastorok 1980b, 1981; Giguère et al. 1982; Riessen et al. 1984; Moore and Gilbert 1987; Moore 1988; Walton 1988), and some have investigated the effect of this predator on community structure (Lynch 1979; Neill and Peacock 1980; Neill 1981; Elser et al. 1987). In this paper we go one step further. We develop a behaviorally based mechanistic model of prey vulnerability that predicts prey selection by *Chaoborus* and can be used to predict the differential impact that this predator has in a zooplankton community. We quantify the parameters of this model through behavioral observations of the predator–prey interaction for a variety of potential zooplankton prey and test the model with independent laboratory feeding experiments. Finally, we apply the model's predictions to help analyze the influence of *Chaoborus* on a simple pond community. These effects are examined both through seasonal changes of predator and prey population densities and in a field enclosure experiment in which predator densities were manipulated.

Model of Prey Vulnerability

The predator–prey interaction between *Chaoborus* and its prey is composed of a series of four successive events, each with a conditional probability of occurrence: encounter (P_e), strike (P_s), contact (P_{con}), and capture (P_{cap}) (Riessen et al. 1984). An encounter, which occurs when the prey enters the more or less cylindrical strike volume surrounding the stationary predator, may or may not result in a strike (attack). A strike may result in either a contact with the prey or a miss, and a contact may result in either a capture (ingestion) or an escape. The probability that an initial strike results in a successful ingestion for *Chaoborus* is usually referred to as the strike efficiency (Swift and Fedorenko 1975; Pastorok 1981). For most crustacean zooplankton prey, including the ones used in this study (pers. obs.), there will typically be no more than one strike in a given encounter; the prey will flee the immediate area if the predator's strike misses (Riessen et al. 1984). The strike efficiency, therefore, is simply the product of P_{con} and P_{cap}. For prey species with little or no evasive reaction (e.g. *Bosmina*), however, there is a relatively high probability of multiple strikes within an encounter, and the strike efficiency must be calculated according to Eq. 3 in Riessen et al. (1984).

Pastorok (1981) quantified prey vulnerability as the product of the encounter rate between predator and prey (a function of P_e) and strike efficiency. This is an indicator of passive selection by the predator, which results from differences in rate of encounter with the prey or in ease of prey capture or ingestion, and not by a decision of the predator (Pastorok 1981; Greene 1983). Often the pattern of prey selection is due strictly to prey vulnerability (Pastorok 1981).

Active selection, where the predator will avoid or reject encountered but potentially ingestible prey (Pastorok 1981; Greene 1983), is indicated by the strike probability, P_s. For *Chaoborus*, this may vary for different prey depending on the hunger level of the predator. Pastorok (1980b) has shown that when *Chaoborus* is well fed, it exhibits active selection for *Diaptomus* over *Daphnia* but that when food is scarce, prey are attacked indiscriminately.

The encounter rate (E) between predator and prey has been derived for *Chaoborus* by Giguère et al. (1982), assuming a cylindrical strike volume, as

$$(1) \quad E = n\bar{s}\pi[(R' \cdot L_t)/2]$$

where n = density of prey, $\bar{s}$ = mean swimming speed of prey, R' = radius of strike volume cylinder, and L_t = length of strike volume cylinder. Thus for a given prey, E will depend on the prey's swimming speed and the size of the predator's strike volume. While R' has been shown to vary between different prey (Riessen et al. 1984), these differences appear to be small compared with observed differences in zooplankton swimming speeds. For the purposes of this model of prey vulnerability, therefore, we assume that strike volumes are the same for the various prey. Relative differences in E are thus determined solely by prey swimming speeds, and relative prey vulnerability can be calculated as the product of strike efficiency ($= P_{con} \times P_{cap}$) and prey swimming speed. Pastorok (1981) also concluded that differences in prey swimming speeds are the main factor affecting encounter rates with *Chaoborus*, and Greene et al. (1986) utilized prey swimming speeds to estimate relative encounter rates with another ambush predator, the ctenophore *Pleurobrachia*.

Is this model of prey vulnerability a good predictor of the order and degree of prey selection by the predator? While this simplified model does not take into account differences in predator choice (P_s) or strike volume, it may still accurately predict prey selection in most situations. Strike volume differences appear to be relatively small, and differences in P_s will only occur if the predator is somewhat satiated. Indeed, Pastorok (1981) has shown that prey vulnerability (for different sizes of *Daphnia*) is a good predictor of prey selection by *Chaoborus* in a natural lake situation. The advantage of this simplified model is that the parameters are easy to determine and indeed have already been calculated for a variety of prey (Swift and Fedorenko 1975; Pastorok 1978; Vinyard and Menger 1980; Swift and Forward 1981; Riessen et al. 1984; Havel and Dodson 1984; Moore and Gilbert 1987; Walton 1988). This model can thus be easily applied to natural situations to determine both the order and degree of prey selection by *Chaoborus*.

Methods

Study Site

Field work in this study was carried out at a small (35 m^2) temporary pond located in the Santa Cruz Mountains near Los Gatos, California. This pond fills with water in November with the onset of the rainy season and retains water until late June; it is completely dry during the summer and early fall. Maximum water depth from December to May varies between 0.6 and 0.9 m; it then decreases rapidly during late May and June (H. P. Riessen, unpubl. data). Water temperature varies between 5 and 15°C during the winter, warms to between 15 and 25°C in May, and then increases up to as high as 29°C in June just before the pond dries (H. P. Riessen, unpubl. data).

The zooplankton community of this pond is relatively simple, consisting of the cladocerans *Daphnia pulex* and *Ceriodaphnia quadrangula*, the calanoid copepod *Diaptomus franciscanus*, the rotifers *Hexarthra* sp. and *Brachionus quadridentata*, and larvae of *Chaoborus trivittatus*. *Chaoborus* is the only major predator in the community. Other potential predators are uncommon or rare; these include some cyclopoid copepods, a

few salamander larvae in the spring, and an occasional water mite or beetle. The temporary nature of this pond precludes the presence of fish. Predation losses among the herbivorous zooplankton are therefore almost entirely due to *Chaoborus*. Another advantage of this small, shallow pond is that it eliminates the spatial complexity of zooplankton distributions found in larger lakes (due primarily to the effects of vertical migration), which might affect encounter rates between predators and prey (see Fedorenko 1975). By eliminating the complicating effects of multiple predator species and the vertical distributional complexity found in large lakes, our pond provides a situation which allows a good assessment of our model and the effect of *Chaoborus* predation on the zooplankton community.

In the experiments and observations described below, *Daphnia* and *Ceriodaphnia* were taken from laboratory cultures that were started with individuals from the temporary pond, and *Diaptomus* and *Chaoborus* were collected directly from the pond. *Diaptomus* adults were used within a few days of their initial collection. They were isolated after being anaesthetized with ether (bubbled into the water) and, although they resumed normal swimming behavior within about 1 min, were allowed to recover for at least 1 h in freshwater before use in an experiment. Fourth-instar *Chaoborus* larvae were individually kept in 50-mL beakers at 18°C and fed a mixture of small *Daphnia* and *Ceriodaphnia* twice a week. They were starved for 1–2 d prior to an experiment.

Components of Prey Vulnerability

P_{con} and P_{cap} were estimated by direct observation of the predator–prey interaction between fourth-instar *Chaoborus* and several prey: adult *Ceriodaphnia* (0.7–0.9 mm, $\bar{X}$ = 0.7 or 0.8 mm), juvenile *Daphnia* (0.7–1.1 mm, $\bar{X}$ = 0.9 mm), and two sizes of adult *Daphnia* (1.1–1.5 mm, $\bar{X}$ = 1.3 mm and 1.7–2.1 mm, $\bar{X}$ = 1.9 mm). A given trial involved observing the interaction between a single *Chaoborus* and 20–40 prey (single species and size at a time) in a small (8 × 8 × 8 cm) glass cube filled with 250–450 mL of water at 21–27°C. Each set of observations occurred under diffuse fluorescent room lighting and lasted between 15 and 60 min. A total of 26 such trials were performed in 1983 and 49 in 1985. The number of strikes, contacts, and captures by *Chaoborus* were recorded for the various prey and used to calculate P_{con} (contacts/strikes) and P_{cap}(captures/contacts). Similar observations have been made by Swift and Fedorenko (1975) and Pastorok (1978) on the strike efficiency of fourth-instar *C. trivittatus*. Their values are included in our calculations of prey vulnerability to provide additional data for both *Diaptomus* and *Daphnia*.

Prey swimming speeds were estimated in two slightly different ways. In 1983, measurements were made in a large petri dish (14.2 cm in diameter) filled to a depth of 1 cm and placed on a grid of 5-mm squares. All animals (about 10 per petri dish at one time) were allowed to acclimate for about 1–1.5 h prior to a trial, which occurred at 22–27°C under diffuse fluorescent room lighting. Mean speed in the horizontal plane was estimated by the number of squares crossed per unit time (minimum of 30 s, measured with a stopwatch). This procedure is similar to the ones used by Swift and Fedorenko (1975) and Pastorok (1980b) to calculate prey swimming speeds.

In 1985, a transparent grid of 5-mm squares was placed against the side of aquaria (water temperature = 21–22°C) containing either *Daphnia* or *Ceriodaphnia*. Animals of a given body length swimming in the vertical plane of the grid were observed and the number of squares they crossed per unit time (minimum of 30 s, measured with a stopwatch) was used to estimate mean swimming speeds.

Prey Selection Experiments

To independently test the predictions of prey selection based on the prey vulnerability model, a series of selection experiments was run using three types of prey that were offered simultaneously to the predator in feeding trials: adult *Ceriodaphnia* (0.7–0.9 mm, $\bar{X}$ = 0.8 mm), juvenile *Daphnia* (0.8–1.0 mm, $\bar{X}$ = 0.9 mm), and adult *Diaptomus* (1.3–1.6 mm, $\bar{X}$ = 1.5 mm). Experiments were run in 0.48-L cylindrical Plexiglas chambers (radius = 3.5 cm, height = 12.5 cm), which had one end detachable from the main body of the chamber and both ends covered with 110-μm Nitex netting (see O'Brien and Kettle (1981) for the exact design). In each trial, 1 fourth-instar *Chaoborus* larva (starved for 2 d) and 10 each of *Ceriodaphnia*, *Daphnia*, and *Diaptomus* were added to a chamber; total prey density was thus 62 individuals/L, a typical value for the temporary pond. Chambers were then incubated in a large aquarium at 18–23°C in the dark for 1 h (1.5 h for two of the replicates). At the completion of this time the chambers were removed and the remaining prey then washed into the netting on the detachable end and counted alive under a dissecting microscope. Twelve replicate experiments were run, each with a control chamber that contained the same prey, but no predator. The number of prey consumed by *Chaoborus* was determined by the number missing from the chamber; the predator's crop at the end of an experiment was visibly filled or mostly filled with this food. All prey in the control chambers were recovered alive and in good condition.

Field Sampling

Quantitative zooplankton samples were collected from the temporary pond during 1 February – 8 June 1984, 18 November 1984 – 12 June 1985, and 2 April – 19 June 1986. Sampling intervals were every 2 wk through the end of April, every 1–1.5 wk during May, and every week during June. A transparent 8.2-L Van Dorn bottle (radius = 7.7 cm, height = 48 cm) positioned vertically in the middle of the water column (horizontally when water depth was very shallow) was used to collect zooplankton. Replicate samples (two during the 1984 season, three during the 1985 and 1986 seasons) were combined into a single sample by filtering the contents through a plankton bucket equipped with 61-μm stainless steel mesh. This small mesh size ensured the complete collection of rotifers, as well as the larger crustacean zooplankton. The contents of the bucket were concentrated and then preserved in 8% formalin. On 12 June and 19 June 1986, three separate replicate samples (each consisting of the contents of two Van Dorn bottles) were taken from the pond. All samples were counted, using standard subsampling procedures (Wetzel and Likens 1979), under a dissecting microscope (Nikon SMZ or Wild M-5).

Field Experiment

In order to directly test the effects of *Chaoborus* predation on the various zooplankton species and the utility of the prey vulnerability model in predicting these effects, a set of enclosure experiments was run in the pond between 12 and 19 June 1986, a time when the density of *Chaoborus* in the pond was

TABLE 1. Calculation of P_{con} (contacts/strikes) and P_{cap} (captures/contacts) for fourth-instar *Chaoborus trivittatus*.

Prey species	Series	Mean prey size (mm)	No. of strikes	No. of contacts	No. of captures	P_{con}	P_{cap}
Ceriodaphnia	1983	0.7	93	47	47	0.505	1.000
Ceriodaphnia	1985	0.8	90	48	47	0.533	0.979
Daphnia pulex	1983	0.9	119	55	49	0.462	0.891
Daphnia pulex	1985	0.9	121	61	58	0.504	0.951
Daphnia pulex	1983	1.3	83	35	27	0.422	0.771
Daphnia pulex	1985	1.9	111	59	15	0.532	0.254

extremely low. The enclosures were transparent Plexiglas boxes (27 × 27 × 25.5 cm; 18.6-L capacity) with a detachable top composed of a Plexiglas frame enclosing 63-μm Nitex netting. Each of the six enclosures received ambient pond zooplankton densities on 12 June 1986 after being filled with a 2-L beaker that was dipped repeatedly in the pond. Twenty fourth-instar *Chaoborus* were added to each of the three experimental boxes; the three control boxes received no *Chaoborus*. The *Chaoborus* used in the experiment were collected from the pond during April 1986 and kept in the laboratory as described above (Study Site section); they were starved for 5 d prior to the initiation of the field experiment.

The enclosures were removed on 19 June 1986 and the contents filtered through the plankton bucket (61-μm mesh) and preserved in a sugar–formalin solution (7.5% formalin and 40 g sucrose/L; see Haney and Hall 1973). Samples were counted as described above. No *Chaoborus* were recovered from the control enclosures, while 14, 15, and 17 intact *Chaoborus* were recovered from the three experimental enclosures; the other added *Chaoborus* either died (body parts recovered) or pupated during the experiment. *Chaoborus* density in the experimental enclosures therefore averaged about 1.0 larvae/L, approximately equal to seasonal peak densities of fourth-instar *Chaoborus* in the temporary pond.

The per capita growth rates (r) of the various zooplankton populations were calculated separately in both control and experimental enclosures from

$$(2) \quad r = \ln (N_t/N_0)/t$$

where N_t = population density (number/litre) in control or experimental enclosures at the completion of the experiment, N_0 = population density (number/litre) at the beginning of the experiment (same for both control and experimental enclosures and determined from field samples on 12 June), and t = duration of the experiment (7 d). For each species, the difference between r in the control enclosures (without *Chaoborus*) and r in the experimental enclosures (with *Chaoborus*) is the per capita mortality rate due to *Chaoborus* predation. This is similar to the process described by Frost (1972), using control and experimental beakers, to calculate grazing rates of *Calanus* on algae.

Results and Discussion

Prey Vulnerability

Differences between the 1983 and 1985 values of P_{con} and P_{cap} for *Ceriodaphnia* and 0.9-mm *Daphnia* (Table 1) were analyzed with 2 × 2 chi-square contingency tests on numbers of contacts and misses resulting from strikes (P_{con} analysis) and numbers of captures and escapes resulting from contacts (P_{cap} analysis). There were no differences between these two years for P_{con} or P_{cap} for either prey ($P > 0.3$). Since these values are

TABLE 2. Strike efficiencies, swimming speeds, and prey vulnerabilities for various prey of fourth-instar *Chaoborus trivittatus*. Relative prey vulnerability for each prey type calculated as product of overall mean values of strike efficiency and swimming speed.

Species	Mean body size (mm)	Source[a]	Strike efficiency	Swimming speed ± SE (mm/s)	Relative prey vulnerability
Ceriodaphnia	0.7	1	0.51	3.92 ± 0.18	1.68
Ceriodaphnia	0.8	2	0.52	2.59 ± 0.13	
Daphnia pulex	0.9	1	0.41	1.23 ± 0.05	0.51
Daphnia pulex	0.9	2	0.48	1.17 ± 0.05	
Daphnia spp.	0.9	3	0.39		
Daphnia pulicaria	0.9	4	0.43		
Daphnia pulex	1.9	1	—	3.56 ± 0.09	0.46
Daphnia pulex	1.9	2	0.14	2.81 ± 0.13	
Daphnia spp.	1.9	3	0.11		
Daphnia pulicaria	1.9	4	0.18		
Diaptomus franciscanus	1.5	1	—	1.83 ± 0.08	0.39
Diaptomus spp.	1.5	3	0.19		
Diaptomus franciscanus	1.5	4	0.24		

[a]1, This study, 1983 results; 2, this study, 1985 results; 3, Swift and Fedorenko (1975); 4, Pastorok (1978).

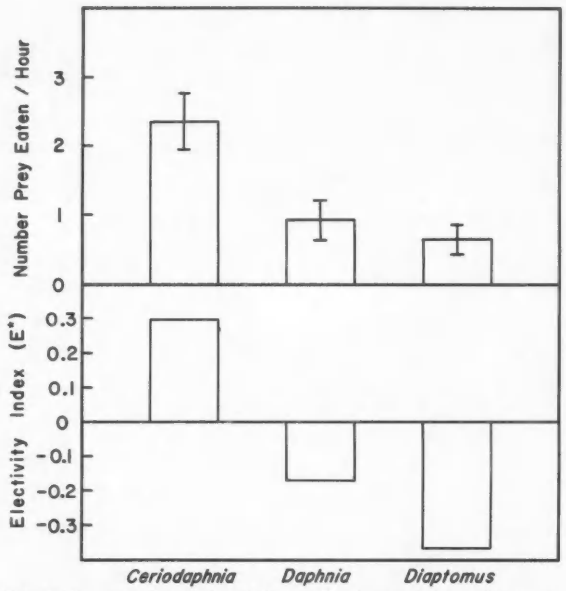

FIG. 1. Prey selection by fourth-instar *Chaoborus trivittatus* larvae on 0.8-mm *Ceriodaphnia*, 0.9-mm *Daphnia*, and 1.5-mm *Diaptomus*. Top panel: predation rate on various prey ($\bar{X} \pm$ SE, $n = 12$). Bottom panel: relativized electivity index, E^* (Vanderploeg and Scavia 1979). Values of E^* between 0 and +1 indicate predator preference, values between 0 and −1 indicate predator avoidance, and no selection is indicated if $E^* = 0$.

independent of the year of observation, the data of the two years are combined for further tests between prey.

Differences in P_{con} and P_{cap} between all four prey types (Table 1) were analyzed with 4 × 2 chi-square contingency tests. P_{con} values varied between 0.42 and 0.53 ($\bar{X} = 0.49$), but the differences were not significant ($P > 0.4$). Regardless of the prey species or size, about half of all strikes resulted in contacts. Riessen et al. (1984) found a similar situation for *Chaoborus americanus*; it had equal success at contacting *Bosmina*, *Daphnia*, or *Diaptomus*, although the values of P_{con} were somewhat lower (0.28–0.38) than those observed for *C. trivittatus* in the present study.

P_{cap} varied inversely with prey body size. Values ranged from 0.99 for the small (0.7–0.8 mm) *Ceriodaphnia* down to 0.25 for 1.9-mm *Daphnia*. Larger cladocerans are more difficult to manipulate and ingest than smaller ones, resulting in lower values of P_{cap} (Swift and Fedorenko 1975; Pastorok 1981; Riessen et al. 1984). The 4 × 2 chi-square contingency test on the P_{cap} data showed a highly significant difference between prey ($P << 0.001$). We subdivided this contingency table into a series of six 2 × 2 chi-square contingency tests to analyze differences between each of the prey by adjusting α according to Bonferroni's inequality to maintain P at 0.05 (Snedecor and Cochran 1980). This analysis showed significant differences ($P < 0.05$) between all pairwise comparisons, except between *Ceriodaphnia* and 0.9-mm *Daphnia* and between 0.9- and 1.3-mm *Daphnia*.

The calculation of relative prey vulnerability for *Ceriodaphnia*, small and large *Daphnia*, and *Diaptomus* (Table 2) is based in our behavioral observations (strike efficiency, swimming speed) and those of Swift and Fedorenko (1975) and Pastorok (1978). *Ceriodaphnia* has the highest prey vulnerability, 3–4 times greater than for the other prey. This is due to its fast swimming speed and high value of P_{cap}, which is a result of small size and a lack of any defensive spines. The other prey are less vulnerable. The strike efficiency on small *Daphnia* is only slightly lower than on *Ceriodaphnia*, but these *Daphnia* are much slower swimmers. Large *Daphnia* swim at the same speeds as *Ceriodaphnia*, but there is a low strike efficiency on them due to a low P_{cap}. The strike efficiency on *Diaptomus* is lower than on *Ceriodaphnia* and these copepods also swim more slowly, resulting in the lowest observed prey vulnerability.

Prey Selection

If prey selection is reflected by prey vulnerability, *Ceriodaphnia* will be the most preferred prey. In addition, our model predicts that *Chaoborus* will eat *Ceriodaphnia*, 0.9-mm *Daphnia*, and 1.5-mm *Diaptomus* in the ratio of their prey vulnerabilities: 4.3:1.3:1.0, respectively.

In the prey selection experiments, *Chaoborus* was highly selective among the prey offered (one-way ANOVA, $P = 0.001$), with adult *Ceriodaphnia* being greatly preferred over both 0.9-mm *Daphnia* and 1.5-mm *Diaptomus* (Fig. 1). *Chaoborus*' predation rate on *Ceriodaphnia* was significantly higher than on each of the other two prey offered (Tukey test, $P < 0.01$); differences between *Daphnia* and *Diaptomus* were not significant (Tukey test, $P >> 0.05$). This preference for *Ceriodaphnia* is also seen in the fact that it had the only positive value of E^*, Vanderploeg and Scavia's (1979) relativized electivity index (Fig. 1).

The prey vulnerability model and several other models are tested against the observed numbers of the various prey eaten in all 12 replicates combined (Table 3). Expected values of the

TABLE 3. Test of expected results of various models of prey selection against observed number of prey eaten in feeding experiments. *$P < 0.05$; **$P < 0.001$.

Prey species	Mean body size (mm)	Observed number eaten	Expected values of model (number eaten)[a]					
			Prey Vuln	D-A Prey Vuln	Strike Eff	Swim Speed	Size	Density
Ceriodaphnia	0.8	29	31.9	30.9	21.8	25.4	20.2	16.3
Daphnia	0.9	12	9.7	10.1	18.1	9.4	18.0	16.3
Diaptomus	1.5	8	7.4	7.9	9.1	14.3	10.8	16.3
Chi-square statistic			0.858	0.476	4.567	4.005	6.560*	15.256**

[a]Prey Vuln = prey vulnerability model; D-A Prey Vuln = density-adjusted prey vulnerability model; Strike Eff = strike efficiency model; Swim Speed = swimming speed model; Size = size model; Density = density model.

prey vulnerability model for the various prey are based on the ratios of prey vulnerability and a total of 49 prey consumed in the prey selection experiments. For example, the expected number of *Ceriodaphnia* consumed according to prey vulnerability is (1.68/2.58) × 49 = 31.9, where 1.68 is the vulnerability of this prey (Table 2) and 2.58 is the total of all prey vulnerabilities combined. The expected values of the model are then compared with the observed values with a chi-square goodness-of-fit test; the smaller the chi-square statistic, the better the fit of expected to observed values. The "density-adjusted" prey vulnerability model (Table 3) takes into account the fact that mean prey densities in the prey selection experiments varied because more of some prey were eaten than others and consumed prey were not replaced. Thus the average number of *Ceriodaphnia* available to *Chaoborus* in these experiments is slightly less than that of the other prey. We take this into account by calculating the "density-adjusted" prey vulnerability (a_i) for each species i:

$$(3) \quad a_i = v_i\,(x_i/c)$$

where v_i = prey vulnerability of species i, x_i = mean number of species i in an experiment, and c = mean number of *Ceriodaphnia* (most vulnerable prey) in an experiment. These adjusted values of prey vulnerability are 1.68 for *Ceriodaphnia*, 0.55 for *Daphnia*, and 0.43 for *Diaptomus*. This adjustment provides for a more accurate test of the prey vulnerability model for the particular set of prey selection experiments that we ran.

For comparative purposes, four other models are tested against the observed values of prey selection in the same manner as the prey vulnerability model (Table 3). The strike efficiency model predicts that prey selection is directly proportional to the relative strike efficiencies on the various prey, and the swimming speed model predicts that prey selection is directly proportional to the relative swimming speeds of those prey. Each of these constitutes only a partial component of prey vulnerability. The size model predicts that prey selection is inversely proportional to prey body size; this follows the generalization that smaller zooplankton are preferentially selected over larger ones by invertebrate planktivores (Dodson 1974; Greene 1983). Finally, the density model predicts that prey selection is directly proportional to the initial densities of the prey, which in the prey selection experiments was equal for all three prey species. This last model can be viewed as a "neutral" model (Caswell 1976) or "null" model (Connor and Simberloff 1986) to examine what happens when none of the components of prey vulnerability or predator choice are taken into account.

The prey vulnerability and "density-adjusted" prey vulnerability models very closely agree with the observed values of prey selection (Table 3). There is no significant difference between the expected values generated by these models and the observed data (chi-square test, $P > 0.6$). The "density-adjusted" model, as expected, provides a slightly better fit to the data. The strike efficiency and swimming speed models, each a component of prey vulnerability, also produce expected values that are not significantly different from observed values, but the fits are not as good (chi-square test, $0.2 > P > 0.1$) as with the prey vulnerability models. The size model is significantly different from the observed data (chi-square test, $P < 0.05$); size alone is therefore a poor predictor of prey selection by *Chaoborus* in mixed-species assemblages (Pastorok 1981). The density model is also significantly different from the observed data (chi-square test, $P < 0.001$), which indicates

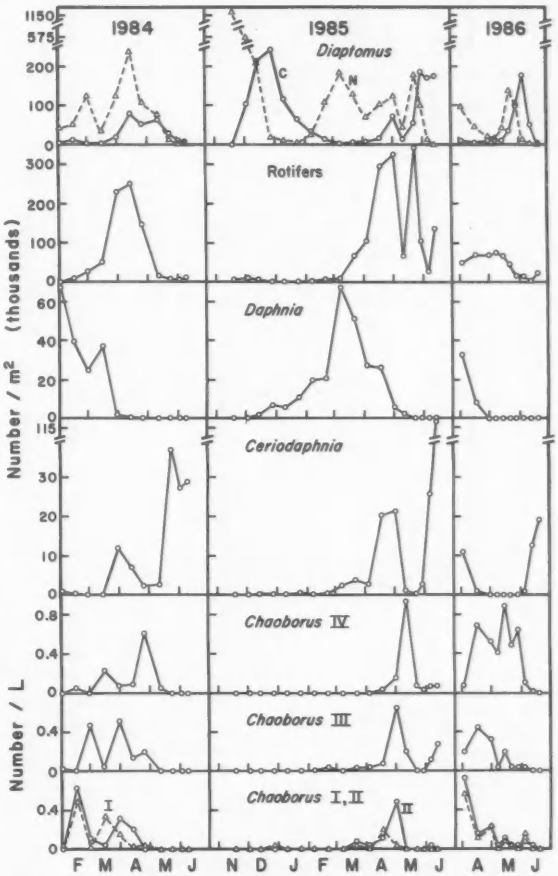

FIG. 2. Seasonal population densities of *Chaoborus trivittatus* larval instars I–IV and the herbivorous zooplankton species in the temporary pond. *Diaptomus* data shows both nauplii (N) and copepodites and adults (C). Rotifers include both *Hexarthra* and *Brachionus*.

significant levels of prey selection. The results of the feeding experiments therefore indicate that prey vulnerability is an excellent predictor of prey selection by *Chaoborus* and that neither strike efficiency nor swimming speed alone is as good a predictor as prey vulnerability.

The ability of prey vulnerability to explain prey selection by *Chaoborus* and other invertebrate planktivores has been previously observed. Pastorok (1981) found that the differential selection of various sizes of *Daphnia pulicaria* by *C. trivittatus* was due to relative vulnerabilities of the prey. *Chaoborus* has a low strike efficiency on large *Daphnia*, and small *Daphnia* (because of slower swimming speeds) have low encounter rates with the predator. Medium-sized *Daphnia* (1.5 mm), therefore, are most vulnerable to *Chaoborus* predation and were selected preferentially by *Chaoborus* in both laboratory feeding experiments and in the lake studied. Greene and Landry (1985) and Greene et al. (1986) investigated predation by two marine invertebrate planktivores on various copepod prey. These workers found that prey selection by both the calanoid copepod *Euchaeta elongata*, a cruising predator (Greene and Landry 1985), and the ctenophore *Pleurobrachia bachei*, an ambush predator

(Greene et al. 1986), was largely determined by differences in prey vulnerability.

Zooplankton Seasonality

Two measures of density are used to illustrate seasonal patterns of the temporary pond zooplankton during 1984–86 (Fig. 2). Densities of the herbivorous zooplankton were calculated in number per square metre; this reflects the population dynamics of these species more accurately than number per litre because as the pond dries in the spring, its volume decreases much faster than its surface area. This relatively large decrease in volume will concentrate the plankton in spring, increasing densities when expressed as number per litre, and leading to errors in estimating changes in population density. *Chaoborus* densities, however, are calculated as number per litre as this best represents the level of predation pressure exerted by this planktivore. The probability of a prey encountering a predator is a function of the number of *Chaoborus* per litre. While the magnitude of the various population peaks of *Chaoborus* and the herbivorous zooplankton species depends on which measure is used, their presence and timing is the same using either number per square metre or number per litre.

The most interesting seasonal pattern present in the community is between *Ceriodaphnia* and fourth-instar *Chaoborus*. In each year, during April or early May, the first of the two seasonal peaks of *Ceriodaphnia* declined rapidly at the time when fourth-instar *Chaoborus* increased to their maximum. The *Ceriodaphnia* population remained very low until the fourth instars declined due to pupation and then increased rapidly to extremely high densities in late May or early June before the pond dried. The timing of the seasonal fall and rise of *Ceriodaphnia* was slightly different in each year, but matched precisely with the peak and subsequent pupation of fourth-instar *Chaoborus*. The spring depression of *Ceriodaphnia* in 1986 was particularly interesting, as it was longer than in the previous years. It matched exactly with the peak of fourth instars, which was also more prolonged in 1986 than in 1984 or 1985, possibly because of cooler water temperatures in this year (H. P. Riessen, unpubl. data).

The seasonal pattern exhibited by *Ceriodaphnia* in this pond is best explained by extremely heavy predation by fourth-instar *Chaoborus*. An early increase of *Ceriodaphnia* is cut short by *Chaoborus* predation, and the prey rebounds only when predation pressure is eased. It is highly unlikely that the population decline of *Ceriodaphnia* during April or early May was due to decreasing food resources as clutch sizes remained relatively constant during this time (H. P. Riessen, unpubl. data). Cladoceran clutch size is mainly determined by the level of nutrition of the female (Green 1956; Hall 1964; Hutchinson 1967) and would therefore reflect any decline in food resources. Heavy predation by *Chaoborus* on *Ceriodaphnia* is predicted by the prey vulnerability model, and the great effect that this predator has on the *Ceriodaphnia* population is expected considering the extreme vulnerability of this prey.

Field Experiment

The field experiment was run in June, a time when *Daphnia* is absent from the plankton. Thus only *Ceriodaphnia*, *Diaptomus*, *Hexarthra*, and *Brachionus* were present in the enclosures. There were no significant differences (*t*-test, $P > 0.4$) in the densities of either rotifer species between experimental (*Chaoborus* added) and control enclosures. *Ceriodaphnia* increased in both the pond and the control enclosures during the experimental period, but decreased in the experimental

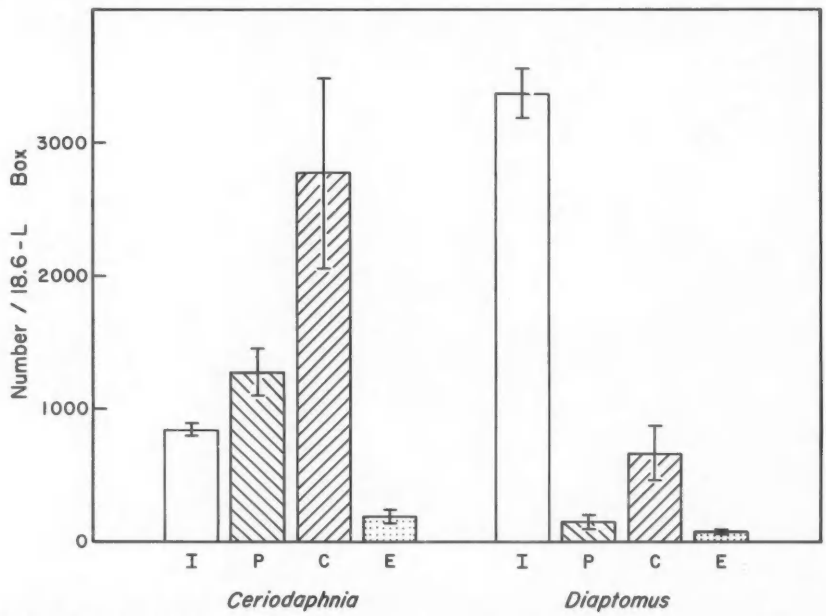

FIG. 3. Results of field enclosure experiment in temporary pond for *Ceriodaphnia* and *Diaptomus*. I = initial densities in enclosures and in pond on 12 June 1986; P = pond densities on 19 June 1986 (equivalent to volume of enclosures); C = final densities in control enclosures on 19 June 1986; E = final densities in experimental enclosures on 19 June 1986. Values are $\bar{X} \pm$ SE, $n = 3$.

enclosures (Fig. 3). The density of *Ceriodaphnia* was 15 times less in the experimental than in the control enclosures, which was a significant difference (*t*-test, $P < 0.05$). The *Ceriodaphnia* mortality rate due to *Chaoborus* predation (calculated from the difference between *r* values in control and experimental enclosures) was $0.388 \cdot \text{individual}^{-1} \cdot \text{d}^{-1}$. *Diaptomus* decreased in the pond and in both sets of enclosures during the experimental period (Fig. 3). Most of these individuals were older copepodites and adults at this time; nauplii were not included in Fig. 3, as they were relatively rare. Despite the decline in *Diaptomus* in the control enclosures, final densities were significantly greater (*t*-test, $P < 0.05$) than in the experimental enclosures (nearly a 10-fold difference). The *Diaptomus* mortality rate due to *Chaoborus* predation was $0.324 \cdot \text{individual}^{-1} \cdot \text{d}^{-1}$.

Although *Ceriodaphnia* was suppressed to a greater extent than *Diaptomus* in this experiment (as would be predicted by the prey vulnerability model), the relative difference in degree of suppression was not as much as predicted by the model (*Chaoborus* induced mortality on *Ceriodaphnia* was only 20% greater than that on *Diaptomus*). This was probably due to the fact that nearly all the potential prey (93% of the *Ceriodaphnia*, 90% of the *Diaptomus*) were eaten by *Chaoborus* in the experimental enclosures. Thus prey selection cannot be accurately determined. In the prey selection experiments, by comparison, only 24% of *Ceriodaphnia* and 7% of *Diaptomus* were eaten. Despite its inability to accurately measure prey selection, the field experiment clearly shows the ability of natural densities of *Chaoborus* to suppress prey populations significantly. The increase in *Ceriodaphnia* in the pond during the experimental period is reflected in the control enclosures, and the ability of *Chaoborus* to reverse this trend is seen in the experimental enclosures. This is a reflection of what happens in the pond as fourth-instar *Chaoborus* peak during April or early May. This field experiment, in conjunction with the seasonal population trends, prey selection experiment, and behavioral observations, points to the profound negative effect that *Chaoborus* predation can have on *Ceriodaphnia*.

General Discussion

Differences in prey swimming speeds largely determine encounter rates with an ambush predator, such as *Chaoborus*, and thus are crucial in determining prey selection (Gerritsen and Strickler 1977). This is often overlooked, as differential prey swimming speeds are relatively unimportant in determining encounter rates for fast cruising predators, such as fish, mysids, and large copepods (Gerritsen and Strickler 1977; Ramcharan et al. 1985). Fast prey that are relatively small (especially if they lack defensive spines) will therefore be the most vulnerable to *Chaoborus*, an invertebrate ambush predator. This explains the extreme vulnerability of *Ceriodaphnia* to this planktivore.

The fast evasive reactions exhibited by copepods (Strickler 1975; Swift and Fedorenko 1975) probably do little to mitigate predation from ambush predators, which remain motionless most of the time and create little or no disturbance for prey to detect (see Greene 1986). Riessen et al. (1984) found that *Chaoborus* was equally efficient at contacting *Diaptomus*, *Daphnia*, and *Bosmina*, prey that exhibit very different evasive reactions. These evasive reactions, however, are probably very important in reducing predation from cruising predators, which create disturbances in the water that prey can detect through mechanoreceptors (Strickler 1975). Thus features of prey which reduce predation from ambush predators may be ineffective against cruising predators, and vice versa.

Large zooplankton are extremely vulnerable to visual fish predators, and heavy fish predation will completely eliminate these conspicuous prey (Brooks and Dodson 1965; Hall et al. 1976). Zooplankton that are both relatively small and fast, such as *Ceriodaphnia*, are extremely vulnerable to *Chaoborus* predation. Relatively high densities of *Chaoborus* (especially third and fourth instars) will completely eliminate these prey. In the temporary pond we studied, the seasonality of *Ceriodaphnia* was largely controlled by *Chaoborus* predation. *Ceriodaphnia* probably only exists at all in this pond because of a very limited seasonal presence of fourth-instar *Chaoborus*, which is due to the temporary nature of the pond. It is able to recover after the period of intense *Chaoborus* predation and produce resting eggs before the pond dries. We would therefore predict that *Ceriodaphnia* cannot coexist in permanent ponds and lakes with sustained high densities of *Chaoborus* (>0.5 individuals/L of large fourth instars). Indeed, Lynch (1979) found that when *C. americanus* was abundant, *Ceriodaphnia* was eliminated from a small Minnesota pond and replaced by *D. pulex*. *Chaoborus* predation in this pond was more intense on *Ceriodaphnia* than on either *Daphnia* or *Diaptomus*, as would be predicted from our vulnerability model. Even at lower densities of *Chaoborus* larvae than were present in our temporary pond or the pond studied by Lynch (1979), however, the effect that this predator has on *Ceriodaphnia* populations, relative to other potential prey, will be large.

When *Chaoborus* feeds opportunistically, striking indiscriminately at all encountered prey (P_i equal for all prey), the model of prey vulnerability developed here will accurately predict both the order and degree of prey selection. This behavior is most likely to occur when prey densities are not exceedingly high and the predator is therefore not satiated (Pastorok 1980b). These conditions probably occur in most situations (Pastorok 1981), but would be especially prominent in oligotrophic and mesotrophic lakes. Most *Chaoborus* undergo a typical diel vertical migration in lakes (Swift 1976; Bass and Sweet 1984), and probably do not feed while near or in the bottom sediments during the day (Swift 1976). They will therefore usually feed opportunistically, at least in the early evening after the resumption of feeding in the water column, even in more eutrophic lakes. Even though feeding history may affect prey selection to some extent, our model was still very useful in analyzing the impact of *Chaoborus* predation in the temporary pond we studied, where prey densities are very high and there is little (if any) room for vertical migration. It accurately predicted the large effect that *Chaoborus* predation has on *Ceriodaphnia* population dynamics. In addition, in our prey selection experiments, each *Chaoborus* ate an average of 4.1 total prey per experiment, enough to completely or mostly fill its crop. Even though the predator was probably becoming satiated by the end of the experiment, the prey vulnerability model accurately predicted both the order and degree of prey selection (Table 3). This model, therefore, may be useful and easily applied in a variety of lakes and ponds. All that is needed is an estimation of strike efficiencies (through simple behavioral observations) and swimming speeds (through observation or filming), and much of this information already exists for fourth-instar *Chaoborus* and a variety of prey (Swift and Fedorenko 1975; Pastorok 1978; Gerritsen 1978; Vinyard and Menger 1980; Swift and Forward 1981; Riessen et al. 1984; Havel and Dodson 1984;

this study). This prey vulnerability model, originally formulated by Pastorok (1981) and further developed in this paper, therefore, has great potential for understanding the role that *Chaoborus* plays in planktonic communities, and will also be useful in developing models of prey selection for ambush predators in general.

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Summer Habitat Utilization and Ecology of Cutthroat Trout Fry (*Salmo clarki*) in Cascade Mountain Streams[1]

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Moore, K. M. S. and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. Can. J. Fish. Aquat. Sci. 45: 1921–1930.

Emergent cutthroat trout fry (*Salmo clarki*) were observed in the margins, backwaters, and side channels, collectively called "lateral habitats," of three study streams with different riparian vegetation. Most fry remained in these lateral habitats until the end of their first summer. The abundance of cutthroat fry was proportional to the area of lateral habitat in each of the study streams. Average size and growth rate of fry were related to the effect of site elevation on stream temperature and the influence of riparian vegetation on the availability of invertebrate food. Lateral habitats are characterized by slow, shallow-water, abundant detritus and benthic invertebrate assemblages of high density. Stream margins and backwaters provide gradients of depth and velocity, cover, and access to food that are appropriate to the habitat requirements of fry. Because fry populations are closely related to the abundance and quality of lateral habitats in small streams, these habitats should be included in the assessment of habitat requirements of cutthroat trout.

Des alevins émergents de la truite fardée (*Salmo clarki*) ont été observés sur les bords, dans les remous ainsi que dans les chenaux latéraux, collectivement désignés sous le terme « habitats latéraux », de trois cours d'eau d'étude à végétation riveraine différente. La plupart des alevins restent dans ces habitats latéraux jusqu'à la fin de leur premier été. L'abondance d'alevins est proportionnelle à la superficie d'habitats latéraux dans chacun des cours d'eau étudiés. La taille et le taux de croissance moyens des alevins montrent un rapport avec l'effet de l'altitude sur la température de l'eau et l'influence de la végétation riveraine sur la disponibilité des invertébrés dont se nourrissent les alevins. Les habitats latéraux sont caractérisés par un écoulement lent, une eau peu profonde, des détritus en abondance et des communautés d'invertébrés benthiques en forte densité. Les remous et les bords des cours d'eau offrent gradients de profondeur et de vitesse du courant, couverture et accès aux aliments qui, tous, répondent aux nécessités de l'alevin en termes d'habitat. Puisque les populations d'alevins sont en étroite relation avec l'abondance et la qualité des habitats latéraux des petits cours d'eau, ces habitats devraient être considérés dans l'évaluation des nécessités en termes d'habitat chez la truite fardée.

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Young-of-the-year cutthroat trout (*Salmo clarki*) are conspicuous inhabitants of slow-water areas near the margins of streams in the Cascade Mountains of Oregon. Low-velocity habitats at the sides of the channel are important geomorphic features of headwater streams that retain nutritional resources and support dense populations of aquatic invertebrates. These lateral habitats are characterized by low-velocity heterogeneous substrate, abundant detritus, and structural protection from high stream discharge, a combination of morphological and hydraulic features that is unique among habitats in mountain streams.

Lateral habitats are important in the early life history of many stream fish, particularly salmonids. Lateral habitats are occupied by the fry of brook trout (*Salvelinus fontinalis*), rainbow trout (*Salmo gairdneri*), and Atlantic salmon (*Salmo salar*) (Keenleyside 1962; Symons and Heland 1978; Reiser and Bjornn 1979), coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) (Lister and Genoe 1970; Everest and Chapman 1972), and cutthroat trout (Bustard and Narver 1975; Aho 1977). These studies have reported the occurrence of salmonid fry in slow water along the margins of stream channels, but none has examined the physical characteristics of lateral habitats or the extent to which they are utilized by fry.

Lateral habitats have not been considered in geomorphic and fisheries classification of stream habitat structure. Stream sections have been classified on the basis of fluvial influences that form predictable sequences of main channel features such as pools and riffles (Keller and Melhorn 1978; Lisle 1986). Geomorphic studies of streams have emphasized main channel habitats that are larger than average stream width (Leopold et al. 1964; Richards 1976) and this level of resolution has been defined as the "channel unit" (Grant 1986). Lateral habitats are a subset of habitats defined at the channel unit scale, are smaller than average channel width, and generally have not been included in studies of geomorphology or fish habitat in streams. Fisheries research has focused on main channel habitats because of the biological significance of pools and riffles as fish habitat and for production of aquatic invertebrates (Chapman and Bjornn 1969; Mundie 1974; Binns and Eiserman 1979). Exclusive consideration of habitat features at the channel unit scale, however, is not sensitive to the habitat requirements of all life

[1]Technical paper No. 8534 of the Oregon Agricultural Experiment Station.

TABLE 1. Physical characteristics of the study streams. Area and relative distribution of habitats in 100-m sections of the study reaches. Habitat area does not include exposed boulders or midchannel structures.

	Study stream		
	Mack	Quartz	Grasshopper
Riparian setting	Coniferous	Deciduous	Open
Drainage area (km²)	5.4	9.7	7.6
Elevation (m)	805	515	880
Channel gradient (%)	10.0	5.3	10.0
Aspect	NNW	SSW	NNE
Stream area (m²)	315	364	371
Pool area (m²)	67	124	103
Percent pool	21	34	28
Riffle area (m²)	193	161	194
Percent riffle	62	44	52
Lateral habitat area (m²)	55	79	74
Percent lateral habitat	17	22	20

history stages of stream fish or appropriate for considering changes in habitat use in response to fluctuations in streamflow. Several studies, for example, have demonstrated the importance of lateral and off-channel areas as rearing and winter habitat for stream fish (e.g. Bustard and Narver 1975; Bisson et al. 1982; Sedell et al. 1982; Hartman and Brown 1987).

The effect of riparian vegetation on fish populations in streams of the Pacific Northwest has been studied by Aho (1977), Murphy and Hall (1981), and Hawkins et al. (1983) and the influence of riparian setting on pool habitat, prey availability, and trout growth was examined by Wilzbach (1985). Greater density and biomass of cutthroat trout was found in open stream reaches, a difference attributed to the effects of increased light on primary production, food availability, and foraging efficiency. These studies generally focused on age 1+ and older fish and main channel habitats. Patterns of habitat use by cutthroat fry and the effects of riparian setting on fry habitats have not been identified.

The objectives of this study were to examine the linkage between cutthroat fry populations and lateral habitats and to determine how habitat utilization and fry behavior change from the time of emergence to the beginning of high streamflow in fall. This study also examined the physical characteristics and nutritional resources of lateral habitats and the possible influences of riparian vegetation on habitat quality, fry growth, and fry population density.

Methods

Study Sites

We investigated the ecology of cutthroat trout fry in third-order streams in or near the H. J. Andrews Experimental Forest in the Cascade Mountains of Oregon. The utilization of lateral habitats by cutthroat trout and the morphology of stream edges were studied in 100-m sections of three streams in different riparian types: a 450-yr-old coniferous stand, a 40-yr-old alder-dominated (*Alnus rubra*) deciduous stand, and an open, herb-, and shrub-dominated site that had been clearcut logged. Study sites were selected at streams with different riparian settings but with similar geomorphic and basin characteristics (Table 1). Cutthroat trout was the only species of fish in the study reaches.

At Mack Creek, the coniferous site, riparian vegetation was dominated by old-growth Douglas-fir (*Pseudotsuga menziesii*)

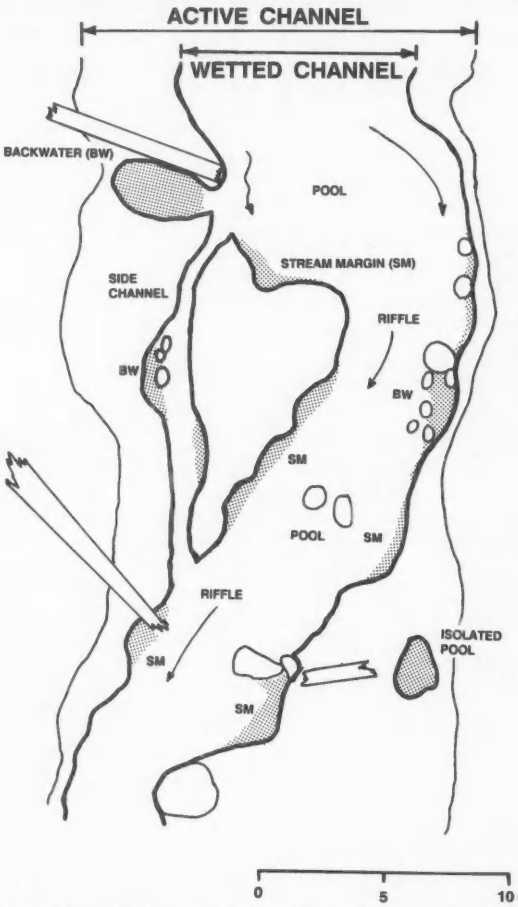

FIG. 1. Habitat structure of a hypothetical stream reach. Lateral habitats are shaded.

and western hemlock (*Tsuga heterophylla*). Quartz Creek, the deciduous site, was logged during the 1940's and red alder has formed a partial canopy over the stream channel. Grasshopper Creek, the open site, was clearcut in 1977 and riparian vegetation was dominated by herbs such as colts-foot (*Petasites frigidus*) and fireweed (*Epilobium angustifolium*) and shrubs such as willow (*Salix sitchensis*).

Stream channel habitat, hydraulics, and substrate were mapped at each site during July and August 1982. Mapping began by constructing a string grid over the active channel surface. The grid was marked at 1-m intervals and used to align a frame of PVC tubing that was placed on the stream bed. Within each square metre delineated by the frame, habitat and hydraulic class, large woody debris, and substrate size distribution were recorded. During the summer of 1983, the distribution of habitats was reevaluated and the availability of substrates and fish cover within lateral habitats was mapped.

The stream at the coniferous site was located in a smaller drainage and had less surface area in the 100-m reach than the streams at either the deciduous or open sites (Table 1). The stream at the coniferous site also had the smallest total area in pool and lateral habitats. Habitat composition of the study reaches was relatively constant from June to October in both

1982 and 1983 (Moore 1987). Coarse woody debris derived from riparian vegetation is a major geomorphic feature in the forested reaches influencing channel structure and creating debris dams. Coarse woody debris was most abundant and evenly distributed at the coniferous site. Remnant debris from the previous coniferous stand was also abundant at the deciduous site. Coarse woody debris was largley absent from the stream channel in the open site, a result of stream cleaning after timber harvest.

Midchannel stream temperature was continuously monitored at each site by recording thermographs. Water temperature and oxygen concentration were measured in 20 lateral habitats at each site after each census of fry populations. Oxygen concentration was measured with a YSI portable oxygen meter calibrated to oxygen saturation for the elevation and temperature of each site.

Stream Habitat Definitions

Because lateral habitats have not been rigorously defined, we developed a classification system based on structural properties of lateral habitats observed in the streams of the Cascade Mountain Range. Lateral habitats are distinguished according to morphology, hydraulics, and orientation to the main channel and classified as stream margins, backwaters, and isolated pools (Fig. 1).

Stream margin habitats are defined as areas of shallow water and slow current along the stream edge without structural separation from the main channel. In stream margins, the long axis of the habitat feature is generally parallel to the main flow. Structures such as boulders and woody debris that deflect flow away from the bank can create abrupt transitions in velocity between stream margins and the main channel. In the study streams, we delineated stream margins as lateral habitats with current velocity less than 4 cm/s and depth less than 20 cm. This combination of depth and velocity coincided with velocity transitions that frequently occur between stream margins and riffles in third-order streams in the Cascade Mountains. This depth was also used arbitrarily to distinguish between stream margin habitat and slow-water areas in adjacent main channel pools. Although stream margins were not physically separated from the main channel, hydrologic exchange between stream margins and the main flow was limited. The movement of water within stream margins may be either an eddy or parallel flow in the main channel.

Backwaters are areas of slowly moving water that are further removed from the influence of the main channel than are stream margins. Backwaters may be isolated pools (off-channel backwaters), or pools connected to the main flow through gaps in the boulders and/or wood that form the habitat. The limited connection to the main flow distinguishes backwaters from stream margins. In backwaters, the opening to the main flow is narrower than the long axis of the habitat. Depth in backwaters and isolated pools may exceed 20 cm. Large boulders and woody debris are the primary structural elements of off-channel backwaters. At high streamflow, most off-channel backwaters become connected to the main channel.

Stream margin and backwater habitats have been described as alcoves, eddys, drop zones, edge pockets, and off-channel pools (Salli 1974; Keller and Swanson 1979; Cummins et al. 1980; Swanson and Lienkaemper 1981; Sedell et al. 1984). We use the term lateral habitat to describe all of these habitat types and the terms stream margin, backwater, and isolated pool to distinguish among each type. Because they are defined in the context of both structure and hydrology, the specific location of some lateral habitats within the active channel may change because of variation in channel hydraulics at different discharges.

TABLE 2. Number of fry observed in 100-m reaches of each riparian site in 1983.

Census interval	Coniferous	Deciduous	Open
June 23	—	16	—
June 26–30	49	67	—
July 7–14	60	24	14
July 22–Aug. 4	42	21	78
Aug. 11–13	—[a]	41	47
Aug. 31–Sept. 3	36	53	46
Oct. 6–8	23	73	69

[a]No census at the coniferous site during this interval.

Observations of Trout Fry

Habitat use, behavior, and population density of cutthroat fry were evaluated by bank survey and underwater observation from June to October 1983. Fry closest to the edge were more effectively observed by bank surveys. Crawling upstream along the bank, looking for fry between and beneath cobbles, was most efficient for observing young fry immediately after emergence and in areas where stream geometry precluded entry of a diver. Fry in pools, riffles, and shallow water near the stream edge were also observed by snorkeling. This approach was more efficient when the diver could look upstream from the lower end of a pool with an unrestricted view of the entire stream width. Fry quickly adjusted to the presence of a diver and usually resumed feeding activity within 30 s from the time the diver entered the stream segment or habitat unit.

Observations of fry distribution were initated when fry started to emerge from the substrate and continued at 2- or 3-wk intervals through the summer growth period. Snorkeling or bank observations were made of all habitats in each reach. Because fry were observed repeatedly throughout the summer, only nondestructive techniques were used to evaluate population size and habitat utilization. Marking or tagging was not used because fry were very small (20–25 mm) and easily injured at the start of the study period. Because no marking was used, mortality, immigration, and emigration of fry in the study reaches could not be measured directly.

Physical characteristics of the habitat were measured where each fish was first observed. If the fish was not disturbed, its position was assumed to be the focal point. The focal point is the position most frequently occupied by an individual fish and is generally the locus of feeding behavior. Velocity was measured with a Montedoro Whitney (folded magnetic field) current meter. Habitat type, stream depth, distance to the nearest stream edge, distance to nearest cover, cover type, and substrate size distribution were also recorded. Use of cover and substrate was determined by direct observation of fry where they maintained focal feeding positions.

At each observation interval, a team of a diver and bank observer worked upstream from the lower end of the reach and attempted to capture each fry they encountered. Fry were captured by slowly moving a small dip net in front of the fish and then placing a meter stick behind the fry and moving closer until the fry was startled and swam forward into the net. This method worked equally well for both diver and bank observer;

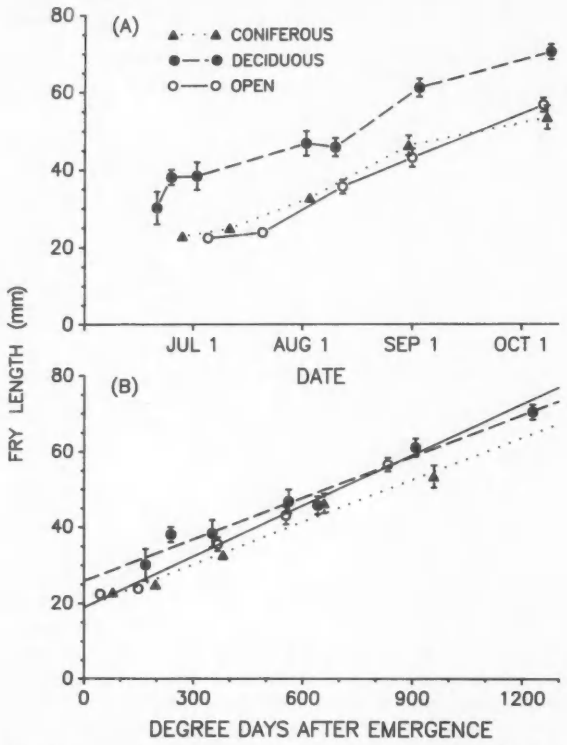

FIG. 2. (A) Fry length from June to October 1983 in the coniferous, deciduous, and open reaches. (B) Fry length versus accumulation of temperature degree days in the riparian study reaches. Coniferous reach fry length $y = 0.037x + 19.0$, $r^2 = 0.982$; deciduous reach $y = 0.036x + 25.8$, $r^2 = 0.972$; open reach $y = 0.045x + 18.8$, $r^2 = 0.980$. Bars are 95% C.I.

95% of capture attempts were successful when the fry first emerged, but capture efficiency decreased to only 70% as the fish grew larger near the end of the study period. After capture, each fry was measured quickly for total length and then returned to the stream at the position where it was first observed. Released fish usually swam to cover in the substrate. We attempted to capture all fry in each habitat unit, but if a fish was not captured, its length was estimated by comparing its size with an adjacent particle in the substrate and then measuring the length of the particle with a small ruler taped to the dip net. Because of the progressive upstream movement of the observation team and the behavior of released fish, it was unlikely that a fish would be counted more than once during each census.

A final census of fry was conducted for all habitats in each reach at the end of the summer season using a combination of electrofishing and snorkeling. Fish were collected by electroshocking, sorted by habitat, and held in buckets until they could be weighed and measured. Any fry not captured by electrofishing were then censused by snorkeling and collected by hand netting.

Benthic invertebrates were sampled from backwaters and stream margins to evaluate the potential for food production at each site. Invertebrates were collected from 10 lateral habitats at each site using a modified Hess sampler with a 250–μm mesh. All samples were processed using a dissecting microscope at 50× magnification. A small sample ($N = 36$) of fry was collected from reaches downstream from the intensive study sections for analysis of gut contents. Fry were collected when they were first observed after emergence, in midsummer, and at the end of summer when they began to occupy different habitats. Each fish was captured with a dip net and immediately preserved in 90% ethanol solution for later dissection and identification of prey items.

TABLE 3. Cutthroat trout fry density in 100-m riparian study reaches in summer (1983). Average number of fry after emergence was complete excluding July 14 and Aug. 3 data from the deciduous reach because of poor conditions for observation. Coniferous, $n = 5$; deciduous and open, $n = 4$.

Site	Reach (fry/100m)	Reach area (fry/m²)	Lateral habitat area (fry/m²)
Coniferous	42.0	0.13	0.76
Deciduous	58.5	0.16	0.74
Open	60.0	0.16	0.81

Results

Fry Populations in the Riparian Study Reaches

Immediately after emerging, fry established territories in lateral habitats that were maintained until the end of summer. The density of fry in each reach was generally highest in early summer after emergence was complete (Table 2). The ability to observe fry varied with weather conditions. For example, overcast and light rain on July 14 and August 3 at the deciduous reach created unfavorable conditions for observation, and comparatively few fry were censused. The combination of electrofishing and visual counts employed in the October census was probably the most efficient method of counting fry. More fry were counted at this census in the deciduous and open reaches than in the preceding census (increases of 38 and 50%, respectively). The reason for the low number of fish captured at the coniferous site could not be determined.

Cutthroat trout fry emerged earliest at the deciduous site, starting by June 1. The first fry at the coniferous site appeared about 3 wk later. Fry at the open reach began emerging about 1 mo after fry in the deciduous reach. Emergence continued for 1–3 wk after the first fry were observed in each stream. The sequence of emergence corresponded to differences in stream temperature during the time trout eggs were developing in the gravel. During the development of trout eggs, average stream temperature was about 5°C warmer at the deciduous site than at the open site and about 3°C warmer than at the coniferous site.

Fry Growth

From June to October, the length of cutthroat fry in the study streams increased threefold and weight increased more than 30-fold. Fry in the deciduous reach emerged earlier and maintained greater average length than fry in the coniferous and open reaches (Fig. 2A). Fry in the open reach had the smallest average length for most of the summer. However, relative to temperature, the greatest rate of increase in fry length was at the open reach (Fig. 2B). Growth rate per degree-day, expressed as the slope of the length versus degree-day regression, was greater at the open site than in either forested reach (test of slope difference $p < 0.05$). Differences in temperature between

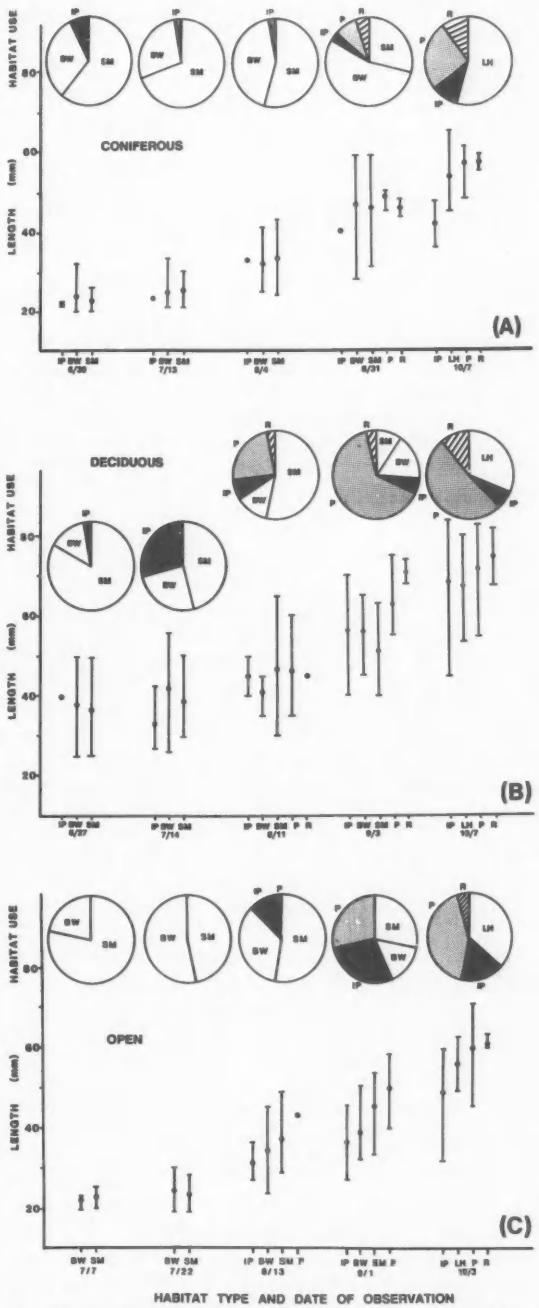

FIG. 3. Changes in habitat use and habitat specific lengths of fry in the (A) coniferous, (B) deciduous, and (C) open reahces. Habitat use expressed as percentage of fry observed in each habitat type. Bars show mean and range of length for each habitat on each date. BW = backwater, IP = isolated pool, SM = stream margin, P = pool, R = riffle, LH = stream margin and backwater combined at final census.

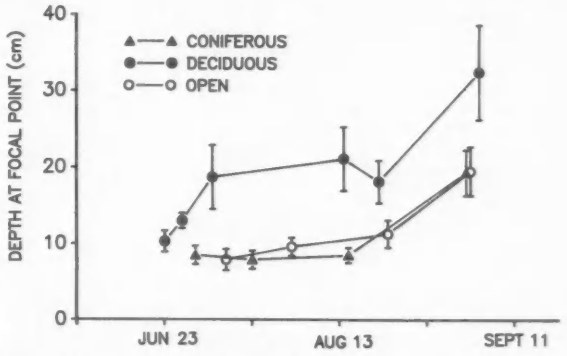

FIG. 4. Stream depth at focal position of fry during June–September 1983 (mean for each site and 95% C.I.).

reaches largely reflected differences in site elevation and were not an influence of shading by the riparian canopy. The sum of mean daily temperature (degree-days) from the time of emergence to final sample was much higher at the deciduous site (1223 degree-days) than at either the coniferous (957 degree-days) or open (831 degree-days) reaches.

Fish condition factor ($K = W/L^3 \times 10^5$) was greater at the deciduous reach than at either the coniferous or open reaches (deciduous>coniferous or open, $p<0.05$, Kruskal–Wallis). Average condition factor was 1.09 at the deciduous site, 0.97 at the coniferous site, and 0.98 at the open site. At the end of summer, total biomass of fry was 0.91 g/m² at the deciduous reach, 0.13 g/m² at the coniferous reach, and 0.39 g/m² at the open reach.

Habitat Utilization

The abundance of fry in each reach was proportional to the area of lateral habitat. The deciduous and open reaches had approximately 30% more lateral habitat and averaged 29% more trout fry than the coniferous reach (Table 3). Fry established territories in lateral habitats that provided visual or spatial distance from other fry. In stream margins, over 85% of the fry occurred as single individuals within a habitat unit. In cases where two or more fry occupied the same stream margin, cobbles and woody debris created complexity and visual isolation within the habitat. In some backwaters, especially off-channel backwaters that physically prevented emigration, fry often occurred in groups. Less than 40% of the fry in off-channel backwaters occurred as single individuals, and as many as 10 fry were observed in one backwater.

All fry occupied lateral habitats exclusively for at least 1 mo after emergence (Fig. 3). The sequence of habitat utilization was the same in each reach. Immediately following emergence, about 65% of the fry were in stream margins, 30% in backwaters, and 5% or less in isolated pools. Fry did not move from these habitats for about 6 wk, but the characteristics of their habitats changed. As discharge decreased during the summer, some stream margins became backwaters, and some backwaters became isolated pools. As a result of lower stream levels, the proportion of backwaters and isolated pools increased relative to total lateral habitat. Because the fry did not move from their initial habitats, the number of fish observed in backwaters and isolated pools increased to about 50% of the total. Fry were not moving from stream margins to backwaters and isolated

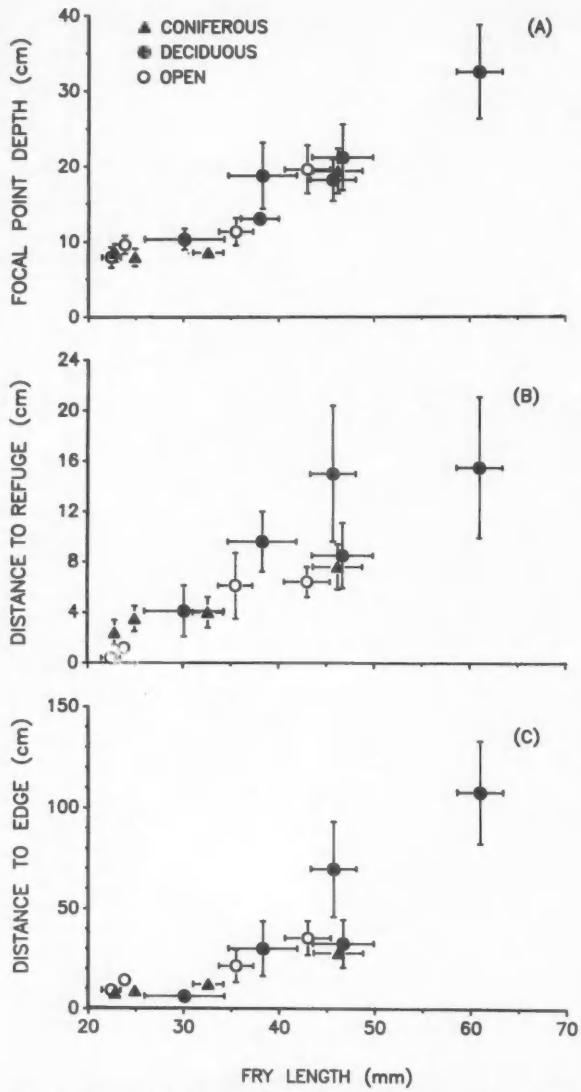

FIG. 5. Changes in (A) focal point depth, (B) distance to refuge, and (C) distance to stream edge associated with increasing length of fry (mean for each site and 95% C.I.).

pools, but rather the stream margins occupied by trout became backwaters and isolated pools as flows decreased.

In late summer, stream discharge was at its lowest level and the contrast between lateral habitat velocity and pool velocity was at its minimum. During this time, some of the larger fry in the stream margins moved to pools. As a result, the proportion of fry in stream margins decreased. Fry in backwaters were less likely to move, and fry in isolated pools could not move to other habitats. The average length of fry was not significantly different among habitat types in the forested reaches (ANOVA, $p > 0.05$), and mortality due to drying of lateral habitats was not observed. In the open reach, fry in isolated pools and backwaters were significantly shorter than fry in other habitats (ANOVA, $p < 0.01$), and some fry were stranded in isolated pools that had become dry.

In October, 65% of the fry remained in lateral habitats at the coniferous reach and 53% remained in lateral habitats at the open site, but only 38% of the fry population were found in lateral habitats at the deciduous reach. Smaller fish stayed closer to the edge in lateral habitats, and the largest fry were most likely to migrate to pools and riffles. Fry at the deciduous reach were larger than in the open or coniferous reaches, and as a result, a larger proportion of the fry population at the deciduous reach moved from lateral habitats to pools and riffles at the end of summer than in the open or coniferous sites.

Fry Behavior and Changes in Focal Point Parameters

Most fry remained in lateral habitats until they were at least 50 mm long, but fry often moved to areas of faster, deeper water within lateral habitats as they grew. Focal point velocity, depth, and distance from the edge increased gradually until fry began to move out of lateral habitats into pools and riffles. With the shift in habitat utilization, focal point parameters increased abruptly. When fry moved from lateral habitats to pools and riffles the average focal point velocity, depth, and distance from the edge increased at least twofold.

Newly emerged fry exhibited swimming behavior (regular tail movements and rheotaxis) at velocities too low to be measured with the current meter (velocity less than 1 cm/s). Fry were obviously responding to velocity differences within lateral habitats, but the velocities were either too low to be measured or occurred in areas that were too small to place the probe of the current meter.

Only fry 30 mm and longer were observed at velocities greater than 1 cm/s. The average focal point velocity never exceeded 2 cm/s in any reach. Many fry, regardless of length, remained in slow water. Fry that moved out of lateral habitats to faster water (>5 cm/s) were generally longer than 55 mm. Only about 35% of the total number of fry were observed at velocities greater than 1 cm/s, and no fry were observed at velocities greater than 15 cm/s.

Fry maintained focal points near, but not on, the stream bottom in areas of shallow water. Fry were first observed in shallow water between 6 and 12 cm deep. Fry moved to deeper water as they grew, but most fry remained in water less than 20 cm deep for at least 6 wk after emergence (Fig. 4). Average focal depth increased rapidly from mid-August to early September, especially at the deciduous reach, but the average depth was always less than 35 cm. Focal point depth was positively correlated with fry length at each site (average depth (cm) $= 0.59 \times$ average length (mm) $- 6.86$, $p < 0.025$, $r^2 = 0.906$, $n = 13$; Fig. 5A). Exceptions to the general pattern of fry length and focal point depth occurred when some of the larger fry remained in shallow water. Many larger fry remained at depths less than 40 cm, but only fry longer than 50 mm were found at depths greater than 40 cm.

Fry usually had a retreat or refuge for avoiding capture. When disturbed, fry moved to crevices in substrates or beneath overhanging boulders and wood. Unless they were further disturbed, fry usually returned to their original focal position within 1 min. Refuges were located within 1–50 cm of the focal point. Newly emerged fry stayed within 5 cm of cover. Distance to cover increased as fry grew, but average distance to cover never exceeded 8 cm at the coniferous and open reaches or 16 cm at the deciduous reach (Fig. 5B). Interstices of cobble and rubble substrate were used as refuges by 30–42% of the fry. Larger substrates and roughness features that formed

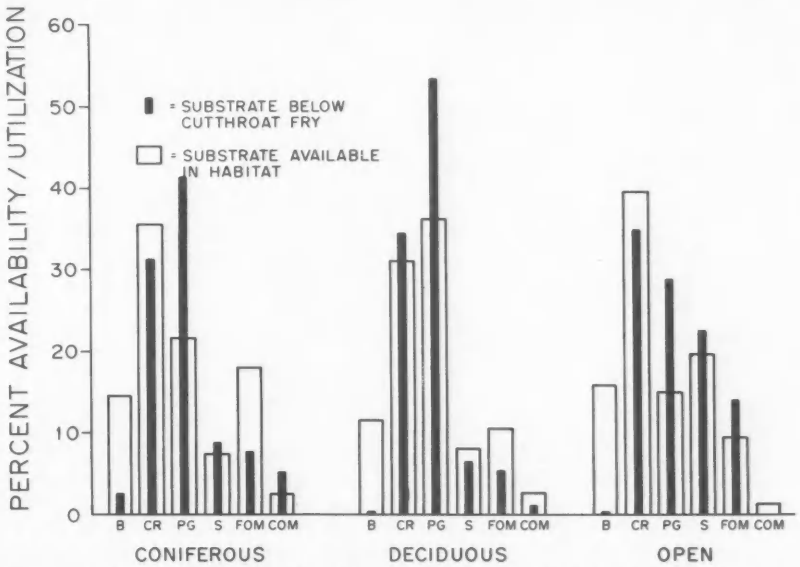

FIG. 6. Substrate composition of lateral habitats and substrate utilization by fry in each of the riparian reaches. B = bedrock, CR = cobble-rubble, PG = pebble-gravel, S = sand, FOM = fine particulate organic matter, COM = coarse particulate organic matter.

TABLE 4. Substrate composition of the wetted channel (WC) and lateral habitats (LH) in summer (percent in each size class). Substrate size classes were sand–FOM (<0.1 cm in diameter), pebble–gravel (0.1–8 cm), cobble–rubble (8–32 cm), and boulder–bedrock (>32 cm).

	Coniferous		Deciduous		Open	
	WC	LH	WC	LH	WC	LH
Boulder–bedrock	56.5	15.1	52.6	12.4	72.5	15.7
Cobble–rubble	24.7	36.2	18.5	31.7	13.3	41.2
Pebble–gravel	11.3	22.3	25.3	36.1	10.4	15.0
Sand–FOM	7.5	26.4	3.6	19.8	3.8	28.1

boundaries of lateral habitat were also frequently used. About 25% of the fry used refuges beneath boulders and 18% escaped beneath large wood debris.

Newly emerged fry were observed within 15 cm of the stream edge at each riparian site. The distance from the focal point to the shoreline increased slowly for most of the summer then increased rapidly when fry began to move to main channel habitats. The increase in distance to the edge was related to increased fry length (Fig. 5C). All fry less than 50 mm long were located within 80 cm of the edge. Conversely, more than 80% of fry 60 mm and longer were located at least 1 m from the nearest stream edge.

Substrate Utilization

Within lateral habitats, cutthroat trout fry were most likely to maintain a focal point that was above heterogeneous substrate. At least 65% of the fry in each stream were observed over mixtures of cobble, rubble, pebbles, and gravel (Fig. 6). Fry were rarely seen in proximity to smooth, homogeneous substrates, such as boulder surfaces or uniform patches of sand or fine particulate organic matter. The extent of selection for substrate size classes within lateral habitats can be compared based

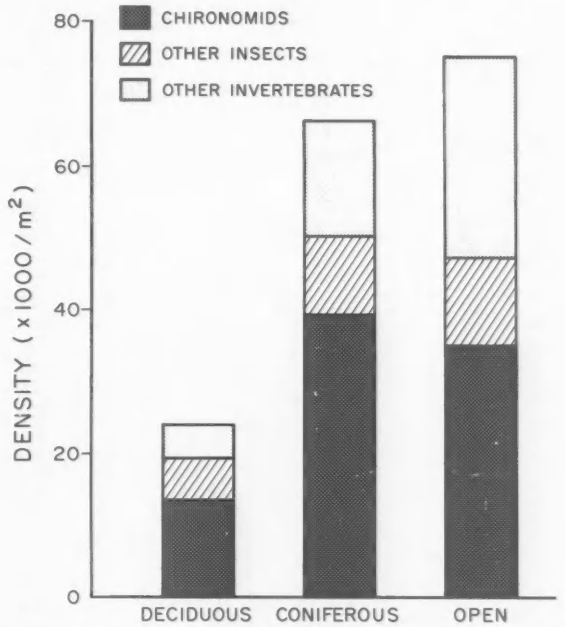

FIG. 7. Abundance of benthic invertebrates in lateral habitats at each of the riparian sites (average of 10 samples at each site collected June 1983).

on substrate utilization and substrate availability. This was measured by a modification of Ivlev's (1961) electivity calculation

$$E = (r - p)/(r + p)$$

where E = electivity, r = proportion of use, and p = proportion in environment. Electivity ranges from -1 to $+1$; -1 indi-

cates the strongest negative selection, +1 indicates the strongest positive selection. Electivity for pebble–gravel substrates was 0.32 at the coniferous reach, 0.19 at the deciduous reach, and 0.44 at the open reach. Electivity for pebble–gravel substrates was greater than for any other substrate class. Differences in electivity between the three reach types were related primarily to differences in the availability of pebble–gravel substrates within lateral habitats (Fig. 6). The open site had the largest value for electivity of pebble–gravel substrate, but this value was influenced by the low availability of this substrate class. Pebble–gravel availability was lowest at the open reach and a greater proportion of fry utilized cobble and rubble substrate than pebble–gravel. Electivity for pebble–gravel substrate was low at the deciduous reach because availability and utilization were both high.

Lateral habitats contained a greater percentage of the substrates associated with high electivity than other habitats of the same reach. Compared with the substrate distribution of the entire wetted channel, lateral habitats had more cobble, rubble, pebble, and gravel substrates (Table 4). Boulders were the most abundant substrate in each of the reaches, but in lateral habitats, substrates in the 1.0- to 16.0-cm size range comprised more than 50% of the surface.

Temperature and Dissolved Oxygen

Water temperature in lateral habitats was always within 1.5°C of the temperature observed in the main channel. Midsummer temperature in isolated pools was expected to be warmer than the main channel because of the long hydraulic residence time in off-channel backwaters. However, there were no temperature differences between isolated pools and the main channel at either of the forested reaches, and isolated pools were generally cooler in summer than the main channel at the open reach. The greatest difference in maximum temperature was at the open site where in August, afternoon temperatures in backwaters averaged 14.4°C and the main channel average was 13.5°C. On the same date, isolated pools were 1°C cooler than the main channel.

Dissolved oxygen concentrations were near saturation in stream margins and backwaters throughout the summer (9.0–11.5 mg O_2/L depending on the elevation and water temperature of each site). Isolated pools were significantly lower in dissolved oxygen than other lateral habitats or the main channel (ANOVA, $p<0.05$), but average oxygen concentrations were never lower than 7.5 mg O_2/L. The lowest oxygen concentration recorded (6.1 mg O_2/L) was taken in early fall at the deciduous site in an isolated pool that was filled with decomposing alder leaves.

Benthic Invertebrates and Diet of Fry

Lateral habitats supported benthic invertebrate communities that were characterized by a high abundance of chironomids, microinvertebrates, and other detritivores (Fig. 7). Chironomid density exceeded 50 000 individuals/m² in some backwaters and average density for all lateral habitats was nearly 30 000/m². Microinvertebrates, predominantly oligochaetes, hydracarinid mites, ostracods, and harpacticoid copepods, had an average density of nearly 20 000/m². Macroinvertebrate populations were dominated by collector–gatherer and shredder functional groups. These insects are associated with the abundant detritus stored in lateral habitats (Moore 1987). Collector–gatherers comprised nearly 80% of the total number of invertebrates in lateral habitats. The collector–gatherer group included the abundant chironomids, but even if chironomids were excluded, collector–gatherers represented more than 50% of the remaining total. Although the average invertebrate density in lateral habitats was comparatively lower at the deciduous site than at either the open or coniferous reaches ($p<0.05$, Kruskal–Wallis), this density represents a relatively high abundance, particularly when compared with pool or riffle habitats in the same reach (R. Wildman, Department of Fisheries and Wildlife, Oregon State University, unpubl. data).

Invertebrate assemblages characteristic of lateral habitats comprised an important part of the diet of fry. Chironomid midge larvae were an especially important food of newly emerged fry. In fry less than 30 mm long, 45–100% of the total number of prey items consumed were chironomid larvae. As fry grew, the percentage of chironomid larvae in the diet decreased ($p<0.01$, $r=-0.567$, $n=36$) but they remained an important food item. In fry of all sizes, chironomid larvae occurred in nearly 90% of the stomachs examined. Fry consumed over 30 different prey taxa, but chironomids, ephemeropterans, and ostracods numerically dominated the gut contents, constituting 88% of the total number.

Discussion

Immediately upon emergence from the gravel, cutthroat trout exhibit adaptive behaviors that position the fish in stream habitats appropriate to the size and metabolic capacity of the fry. Stream margins and backwaters are particularly suited to the habitat requirements of cutthroat trout fry, providing appropriate gradients of depth and velocity, cover, and access to invertebrate food. Because fry do not move for several months once they establish territories in lateral habitats, the quality of the habitat is critical for growth and survival.

Many stream salmonids occupy the highest velocity water their swimming ability and the availability of velocity shelter will allow, thereby increasing their exposure to drifitng prey (Chapman and Bjornn 1969; Lister and Genoe 1970; Fausch 1984). The movement of cutthroat fry from areas of slow current in early summer to faster water in pools and riffles at the end of summer is consistent with this concept. The hydraulic properties of lateral habitats create areas of low velocity particularly suited to the requirements of newly emerged fry. Subsequent changes in focal point depth, distance to the edge, and distance to refuge in cutthroat trout fry are related to increased swimming ability with growth.

Riparian Influence on Fry Populations

Riparian vegetation and the effect of site elevation and aspect on water temperature were important influences on cutthroat trout fry populations. Growth rate was highest at the open site, but the average size was greatest at the deciduous reach. Fry at the coniferous site had the smallest average size and poorest condition factor. Productivity of lateral habitats, access to invertebrate prey, and temporal stability of habitat characteristics are all potentially influenced by the effect of riparian vegetation on energy inputs and channel structure (Swanson et al. 1982; Wilzbach et al. 1986; Moore 1987).

The higher growth rate of cutthroat fry at the open reach may have resulted from the effect of increased light on primary production, invertebrate production, and prey capture efficiency. Open sites have a higher standing stock of benthic algae (Lyford

and Gregory 1975; Moore 1987) and a greater abundance of herbivorous, multivoltine invertebrates (Grafius 1976; Hawkins et al. 1983). Because of the short generation time of these animals, production relative to standing stock may be greater than at sites with detrital based invertebrate assemblages. The coniferous site also had a high standing stock of invertebrates, however; this food source may be less available to fry because shading by the canopy may reduce the ability of fry to locate and to capture prey. Foraging efficiency of trout was lower in streams in old growth forests than in streams with more open riparian settings (Wilzbach 1985).

Fry at the deciduous reach may have been larger because of the effect of temperature on the timing of emergence and the metabolic efficiency of fry. For rainbow trout, development of eggs to hatching requires 50 d at 7.3°C and 25 d at 12°C (Bardach et al. 1972). If cutthroat trout eggs develop at a similar rate, eggs spawned at the same time would hatch 2–3 wk earlier at the deciduous reach than in the other reaches. This interval corresponds to the sequence of initial observations of fry in each of the reaches. In a similar manner, the increased stream temperature associated with an open canopy has accelerated the development of eggs and timing of emergence of coho salmon in Carnation Creek, British Columbia (Scrivener and Andersen 1984).

As stream temperatures increase from 5 to 15°C, the difference between standard metabolism and active metabolism increases 1.5 times in cutthroat trout (Dwyer and Kramer 1975). Defined as "scope" for activity and growth (Fry 1947), this difference means that a greater portion of food energy is available for growth and less is required for standard metabolism than at colder temperatures. This relationship only applies when food is abundant (Bisson and Davis 1976; Wurtsbaugh and Davis 1977), and the standing crop of invertebrates at the deciduous reach was lower than in the other reaches. However, this apparent contradiction may not apply to the deciduous reach. Warmer temperatures at the deciduous reach may shorten invertebrate generation time and increase invertebrate production relative to standing stock biomass (Benke 1984). This effect of temperature particularly applies to midges and *Baetis* mayflies (Mackey 1977), the most important food of fry in these streams.

Habitat Complexity

The formation and maintenance of lateral habitat is dependent on structures that divert streamflow and create spatial and hydraulic diversity at the channel margin. Such complexity is derived from the geomorphic structure of the valley floor, large boulders, and large woody debris. Geomorphic features that create edge complexity and form fry-rearing habitat in summer also create the largest and most persistent refuge habitat in winter (Moore 1987). Debris dams and large wood along the margin of the channel create lateral habitats that undergo smoother, more predictable changes in volume and velocity with increased streamflow than do lateral habitats formed by boulders and cobbles. At the open site, lateral habitats are formed by boulders without the additional stabilizing influence of large woody debris. The open site, however, has an abundance of boulders, many more than 3 m in diameter. In drainages not supplied with large boulders, removal of the canopy and woody debris from the channel may result in reductions in the quality of lateral habitats and lower populations of fry and adult fish.

Attempts to increase winter carrying capacity by enhancing winter habitat require structures that are not only appropriate for the behavior of the fish, but are also appropriate to the behavior of the stream. Artificial off-channel habitats have been used by salmonid fry in small streams (Bustard and Narver 1975), but experimental refuges have often failed because they could not withstand high flows or have served as sediment traps during bedload movement (Mason 1976). Habitat "improvement" directed at increasing pool depth at the expense of edge heterogeneity may reduce fry populations and decrease winter carrying capacity for all age classes (Everest et al. 1984).

Incorporation of Lateral Habitats into Stream Habitat Models

Because habitat requirements of cutthroat fry change significantly during the summer and throughout the year, models that prescribe habitat parameters based on limited probability-of-use data, such as Instream Flow Methodologies (Bovee and Cochnauer 1977), may inadequately consider the habitat requirements of fry populations. The focal point velocities measured in this study were much lower than velocities described for cutthroat trout fry in a habitat suitability index proposed by Hickman and Raleigh (1982). Such indices may be improved if they incorporate the utilization of areas of very low velocity by recently emerged fry. Instream flow models have also focused on the effects of changing flow on main channel habitats and relatively uniform cross sections (Bovee 1982; Morhardt 1986). As a result, they are not sensitive to the complexity of habitat structure characteristic of the margins of small streams or to the rapidly changing habitat requirements of cutthroat fry.

Management of stream salmonids must recognize temporal changes in habitat utilization within both cohort and population. Fishery biologists and geomorphologists alike have focused on the characteristics of main channels and have largely ignored the unique properties of channel margins and secondary channels in small streams. But like floodplain ponds, sloughs, and secondary channels in large rivers (Sedell et al. 1984; Welcomme 1985), lateral habitats in streams make a unique contribution to fishery resources because they increase habitat diversity and provide rearing areas and refuge from high flow. The reduced velocities, shallow depths, and greater complexity of these lateral areas of the active channel contribute to their ecological importance as depositional zones for organic matter, rearing areas for invertebrates and fish, and refuges for most stream organisms during floods. Stream margins, backwaters, and secondary channels are critical habitats for the fry of many salmonids, and these lateral areas provide the major rearing habitat for cutthroat trout in streams of the Cascade Mountains of Oregon.

Acknowledgements

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Fish Species Richness in Relation to Lake Area, pH, and Other Abiotic Factors in Ontario Lakes

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Matuszek, J. E., and G. L. Beggs. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.

Survey data from 2931 Ontario lakes were analyzed to determine how fish species richness was empirically related to a set of 19 physical and chemical limnological variables. Lake area was the dominant factor, explaining 18% of the variation in species number. Total aluminum, latitude, dissolved organic carbon, and elevation together explained an additional 16%. The strong relationship between species number and lake area was quantified using lakes with pH ≥ 6.4 and then applied to all the surveyed lakes to estimate species number. Deviations from the expected values indicated that species number decreased with decreasing pH below 6.0, resulting in significantly fewer species in lakes with pH < 6.0. In the subset of lakes with pH < 6.0, pH alone explained 21% of the variation in species number; elevation, lake area, and dissolved organic carbon together explained an additional 20%. Interactions between pH and lake area were identified; lake size decreased significantly both at low pH (<6.8) and at high pH (≥7.7). An understanding of these interactions was essential in explaining the relative roles of pH and lake area in determining species richness.

Les auteurs ont analysé les données de relevés de 2 931 lacs de l'Ontario afin d'examiner la relation empirique entre la diversité des espèces de poisson et un ensemble de 19 variables limnologiques physiques et chimiques. Le facteur dominant était représenté par la superficie des lacs, qui expliquait 18 % de la variation du nombre d'espèces. Un autre 16 % pouvait être expliqué par la teneur en aluminium total, la latitude, la teneur en carbone organique dissous et l'altitude. La forte relation entre le nombre d'espèces et la superficie des lacs a été quantifiée en utilisant les lacs à pH ≥6,4. Elle a ensuite été appliquée à l'ensemble des lacs étudiés afin d'estimer le nombre d'espèces. Les écarts aux valeurs prévues montraient que le nombre d'espèces diminuait en fonction de la baisse du pH, en-deçà de 6,0, de sorte que le nombre d'espèces était significativement inférieur dans les lacs à pH inférieur à 6,0. Dans le sous-ensemble de lacs à pH <6,0, le pH expliquait à lui seul 21 % de la variation du nombre d'espèces. L'altitude, la superficie et le carbone organique dissous en expliquaient ensemble un autre 20 %. Les auteurs ont déterminé les interactions entre le pH et la superficie des lacs; la superficie des lacs diminuait de façon significative tant à des valeurs de pH faibles (<6,8) qu'élevées (≥7,7). La connaissance de ces interactions s'avérait essentielle pour expliquer les rôles relatifs du pH et de la superficie des lacs au cours de la détermination de la diversité des espèces.

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The loss of fish populations from acidified lakes and rivers has been observed by investigators in Canada, Scandinavia, and the United States (Beamish and Harvey 1972; Harvey 1975; Wright and Snekvik 1978; Schofield 1982; Watt et al. 1983). Low pH and related chemical conditions, such as elevated concentrations of aluminum, have been implicated in the loss of these fish populations (Haines 1981; Baker and Schofield 1982). The differential tolerance of fish species to low pH (Beamish and Harvey 1972; Haines 1981; Rahel and Magnuson 1983) suggests that as a lake acidifies the community composition will change and the number of fish species present will be reduced. This process has been documented by researchers compiling case histories of acidifying lakes (Beamish et al. 1975; Beamish 1976; Schindler et al. 1985) and is inferred from the survey results of lakes spanning a gradient of pH (Harvey 1975; Somers and Harvey 1984).

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The relationships between lake pH and the number of fish species and between lake area and the number of fish species have been determined for several regional data sets (Barbour and Brown 1974; Harvey 1975, 1978; Rahel and Magnuson 1980; Rahel 1986). Such relationships have been used to estimate the number of fish populations lost due to acidic deposition (Harvey and Lee 1982; Somers and Harvey 1984). However, small lakes generally support fewer fish species than large lakes (Barbour and Brown 1974; Tonn and Magnuson 1982; Rahel 1986), and lakes of low pH are also frequently small in size (Eilers et al. 1984; Rago and Wiener 1986). It is possible, therefore, that the relationship reported between fish species number and lake pH may be confounded by other covarying factors, especially lake area. Only two recent studies have dealt explicitly with the effects of lake area and lake pH on fish species richness (Rago and Wiener 1986; Eadie et al. 1986).

In this paper we use a large data set (2931 Ontario lakes) to examine the relationships among fish species number, lake pH,

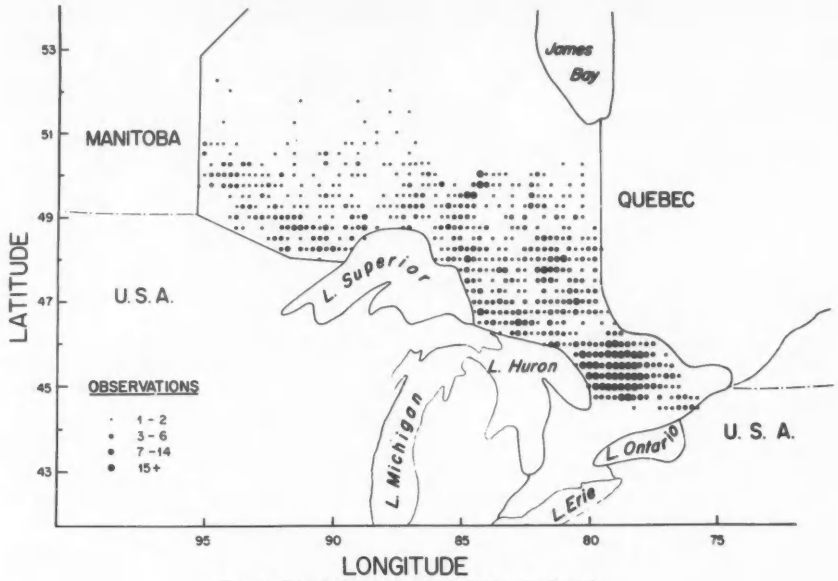

FIG. 1. Distribution of sampled lakes in Ontario.

TABLE 1. Measured variables, number of lakes sampled, and method of determination (Dodge et al. 1985; Ontario Ministry of the Environment 1981).

Variable	*N*	Method
Species number	2931	Gill nets, seine nets, minnow traps
Latitude	2931	Topographic maps
Longitude	2931	Topographic maps
Lake area (ha)	2930	Planimeter, grid overlay
Maximum depth (m)	2930	Soundings, contour maps
Mean depth (m)	2913	Volume/lake area
Elevation (m)	2931	Topographic maps
Secchi depth (m)	2856	20-cm disc
pH	2914	pH meter at room temperature
Alkalinity ($mg \cdot L^{-1}$)	2872	Titration for inflection point
Conductivity ($\mu \cdot cm^{-1}$)	2666	Conductivity meter at 25°C
Apparent colour (Hazen units)	1549	Colorimeter, includes dissolved and suspended substances
DOC (mg/L)	1256	Colorimetric measurement of CO_2 produced
Calcium ($mg \cdot L^{-1}$)	1735	Atomic absorption
Magnesium ($mg \cdot L^{-1}$)	1648	Atomic absorption
Sodium ($mg \cdot L^{-1}$)	1512	Atomic absorption
Potassium ($mg \cdot L^{-1}$)	1529	Atomic absorption
Sulphate ($mg \cdot L^{-1}$)	1631	Calorimeter, ion chromatography
Total aluminum ($mg \cdot L^{-1}$)	1490	Atomic emission or absorption
Manganese ($mg \cdot L^{-1}$)	1508	Atomic emission or absorption

and lake area. We also contrast the degree to which lake area, pH, and other abiotic factors influence fish species richness.

Methods

Data Base Description

The sampled lakes are located in Ontario on the precambrian bedrock of the Canadian Shield (44–51°N, 76–95°W) (Fig. 1) in a region that contains many deep, clear, coldwater, oligotrophic lakes. Major large fish species include lake trout (*Salvelinus namaycush*), brook trout (*Salvelinus fontinalis*), smallmouth bass (*Micropterus dolomieui*), walleye (*Stizostedion vitreum*), lake whitefish (*Coregonus clupeaformis*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), and white sucker (*Catostomus commersoni*). The three main fish community groupings found in Ontario lakes are described as Salmonid–Percid, Brook Trout, and Centrarchid by Minns (1986).

Annual loadings of acids from precipitation range widely across the sampled region. In the southeast part of the province, lakes remote from point sources receive greater than 30 kg $SO_4^{2-} \cdot ha^{-1} \cdot yr^{-1}$ (wet deposition) whereas lakes in the northwest receive less than 10 kg $SO_4^{2-} \cdot ha^{-1} \cdot yr^{-1}$ (Tang et al. 1986). Many of the low-pH lakes are located near large SO_2 sources in Sudbury (46°30′N, 81°00′W) and have received very high acid loadings in the past (Keller and Pitblado 1985).

Up to 20 variables were measured for each lake in the data set (Table 1).[2] Most of the surveyed lakes have data for species number, latitude, longitude, lake area, mean and maximum depth, elevation, Secchi depth, pH, alkalinity and conductivity. Data for the remaining chemical variables exist for a substantially smaller number of lakes.

Fish species presence was determined between the late 1960's and 1981 as part of the Ontario Aquatic Habitat Inventory (AHI) survey. Lake surveys were conducted between June and September and generally lasted 3–5 d. Surveys were designed to sample all fish habitats. Primary gear types were variable mesh gillnets (minimum of eight randomly assembled 15 × 1.5 m panels varying in mesh sizes between 25- and 140-mm stretched mesh), seine nets (small mesh <8 mm), and baited minnow traps. These were set according to methods outlined in Dodge et al. (1985).

Water samples for chemical analysis were collected between 1978 and 1984. Each lake was sampled once during this period,

[2]Survey methods and the data are described in more detail in Green et al. (1987). A copy of the data set can be obtained from the Fish Community and Habitat Section, Fisheries Branch, Ministry of Natural Resources, 99 Wellesley St. W., Toronto, Ont. M7A 1W3.

TABLE 2. Median, minimum, and maximum values for each variable in the stepwise multiple regressions of $\log_{10}$ (species number + 1) on all variables.

Variable	All sampled lakes		Lakes with pH < 6.0	
	Median	Range	Median	Range
Species number	5	0–24	5	0–15
Latitude	45°45′	44°40′–50°30′	45°33′	44°52′–47°30′
Longitude	79°14′	77°35′–87°39′	79°08′	78°06′–81°40′
Lake area (ha)	45.4	0.9–3157.5	22.7	0.9–2023.0
Maximum depth (m)	13.7	0.9–88.5	11.2	0.9–88.5
Mean depth (m)	4.5	0.5–32.1	4.1	0.7–32.1
Elevation (m)	366	130–549	396	168–518
Secchi depth (m)	3.7	0.7–20.9	3.4	0.7–20.9
pH	6.39	4.43–9.92	5.65	4.43–5.99
Alkalinity ($mg \cdot L^{-1}$)	4.0	−1.9–249.7	1.1	−1.9–12.5
Conductivity ($\mu mh \cdot cm^{-1}$)	37	16–499	30	6–76
Apparent colour (Hazen units)	28.7	−3.2–352.0	32.0	−3.2–197.0
DOC ($mg \cdot L^{-1}$)	4.5	0.1–58.0	4.0	0.1–13.4
Calcium ($mg \cdot L^{-1}$)	3.3	1.0–64.3	2.5	1.0–13.6
Magnesium ($mg \cdot L^{-1}$)	0.9	0.2–19.3	0.6	0.2–4.0
Sodium ($mg \cdot L^{-1}$)	0.75	0.25–2.0	0.60	0.25–2.00
Potassium ($mg \cdot L^{-1}$)	0.44	0.10–1.8	0.38	0.18–1.12
Sulphate ($mg \cdot L^{-1}$)	7.4	0.6–20.0	7.8	2.6–20.0
Total aluminum ($mg \cdot L^{-1}$)	0.033	0.002–0.5	0.085	0.004–0.540
Manganese ($mg \cdot L^{-1}$)	0.025	0.002–0.2	0.038	0.003–0.286

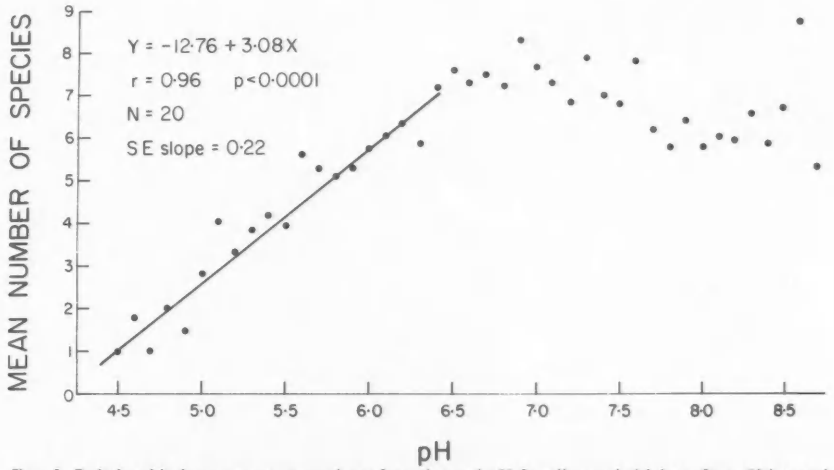

FIG. 2. Relationship between mean number of species and pH for all sampled lakes. One pH interval spans 0.1 unit; for example, interval 6.0 includes lakes with $6.0 \leq pH < 6.1$. The number of lakes per interval, starting at pH 4.5, is 6, 5, 4, 10, 11, 16 (pH 5.0), 20, 28, 23, 35, 47, 59, 60, 90, 77, 125 (pH 6.0), 110, 123, 129, 127, 116, 130, 118, 122, 122, 119 (pH 7.0), 94, 102, 94, 91, 89, 83, 98, 75, 65, 75 (pH 8.0), 58, 48, 37, 34, 14, 12, and 7.

mainly during the summer, fall, or winter. These samples were primarily (85%) tube composite samples, collected at midbasin and extending to a depth of 5 m, or 1 m from the bottom in shallow lakes. Approximately one third of the measurements for pH, inflection point alkalinity, and conductivity were done in field stations according to methods outlined in Goodchild et al. (1981). The remaining chemical analyses were done in federal and provincial government laboratories according to methods described in Environment Canada (1979) and Ontario Ministry of the Environment (1981), respectively.

Because fish sampling and water chemistry sampling were part of different survey programs, the sampling dates for individual lakes generally do not coincide. Fish sampling was done within 5 yr of the chemistry sampling for 27% of the lakes, within 10 yr for 69% of the lakes, and within 15 yr for 98% of the lakes. For lakes remote from large SO_2 point sources, such as Sudbury, there is little evidence of significant changes in pH over the periods in question (Dillon et al. 1987). Therefore, it seems reasonable to associate the pH values with the species data for these lakes. However, in the Sudbury area, Keller and Pitblado (1985) found average increases of 0.3 pH unit in low-pH (<5.5) lakes over 5- to 7-yr periods after 1970. Furthermore, Conroy et al. (1975) found elevated heavy metal concentrations (>30 $\mu g \cdot L^{-1}$ Ni, >25 $\mu g \cdot L^{-1}$ Cu) within a distance of approximately 80 km from Sudbury. The lakes in our data set are generally beyond this distance from the smelter.

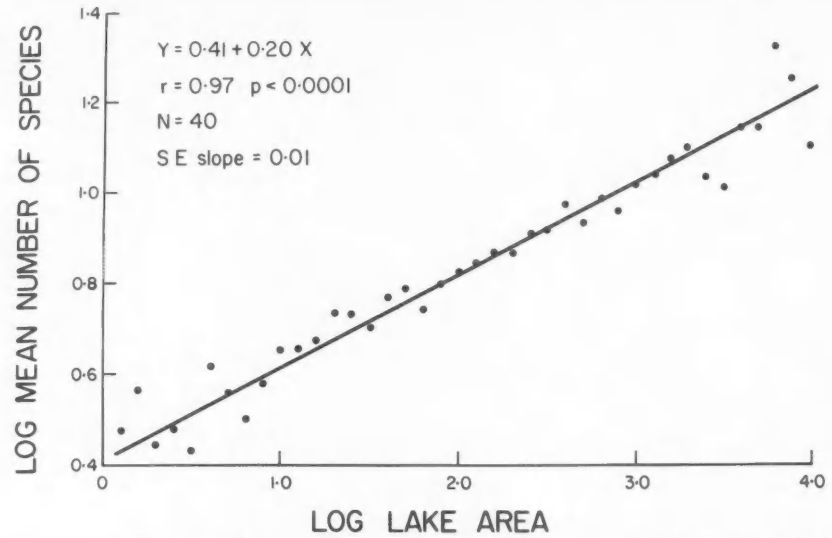

FIG. 3. Relationship between $\log_{10}$ mean number of species and $\log_{10}$ lake area for lakes with pH $\geq$ 6.4. One lake area interval spans 0.1 unit on the $\log_{10}$ scale; for example, interval 2.0 includes lakes with $2.0 \leq \log_{10}$ lake area < 2.1. The number of lakes per interval, starting at 0.1, is 6, 6, 5, 14, 15, 19, 28, 26, 38, 45 (1.0), 54, 54, 49, 75, 64, 89, 84, 104, 128, 95 (2.0), 111, 93, 109, 79, 81, 69, 73, 47, 51, 48 (3.0), 43, 24, 37, 15, 17, 7, 8, 7, 4, and 7 (4.0).

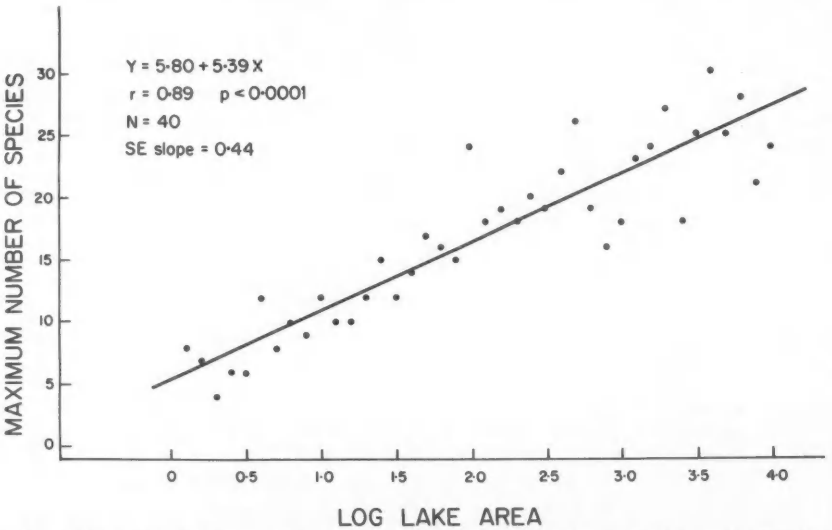

FIG. 4. Relationship between maximum number of species and $\log_{10}$ lake area for lakes with pH $\geq$ 6.4.

To test the validity of incorporating the Sudbury area data in our analyses, we compared a plot of fish species number versus lake pH for lakes near Sudbury with a similar plot for lakes remote from Sudbury. No systematic or extraordinary deviations were evident; therefore, these data were retained in our data set.

Data Analysis

An initial plot of species number versus pH suggested a limiting effect on fish species number at low pH. However, there was substantial variation in species number among lakes with similar pH values. Therefore, lakes were grouped by pH interval (0.1 unit), and the mean number of fish species was calculated for each interval. An initial pH threshold of 6.4 was identified below which mean species number declined. The relationship between fish species number and lake pH was quantified by regressing the mean number of fish species on pH interval. Since the number of lakes in each interval varied, each observation in the regression was weighted by the reciprocal of the variance of the mean number of fish species to account for differences in reliability.

To assess the effects of lake area, independent of lake pH, lakes with pH values above the apparent pH threshold of 6.4 were examined. These lakes were grouped by lake area interval

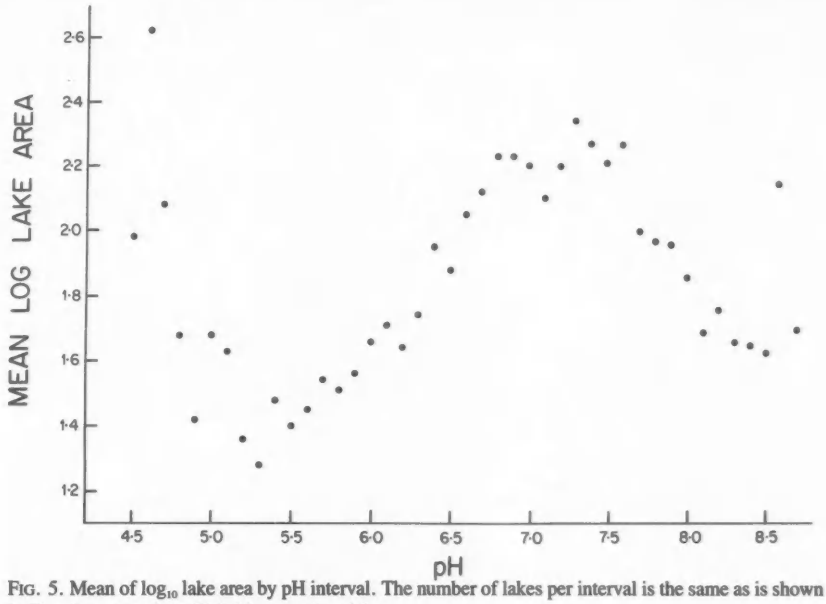

FIG. 5. Mean of $\log_{10}$ lake area by pH interval. The number of lakes per interval is the same as is shown in Fig. 2, except that pH 6.6 has one less lake.

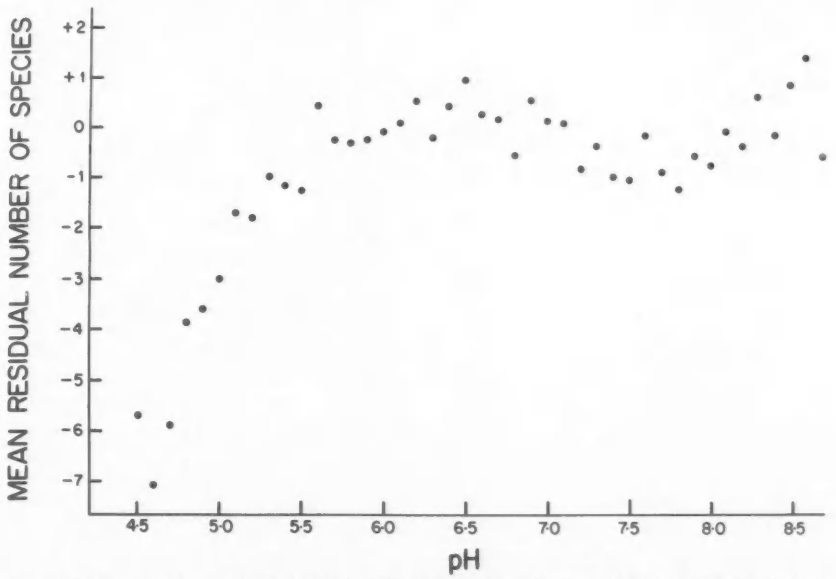

FIG. 6. Mean residual number of species by pH interval. The residual number of species for a lake is the deviation of the observed number from the number predicted by lake area. The number of lakes per interval is the same as is shown in Fig. 2, except that pH 6.6 has one less lake.

(0.1 unit on the $\log_{10}$ scale), and the mean number of fish species was calculated for each interval. A weighted regression was used to quantify the relationship between fish species number and lake area interval. Log_{10} transformations of both the dependent and independent variables produced the most linear relationship, as judged by examination of the residuals.

The relationship between lake pH and lake area was examined using the Spearman correlation coefficient and a plot of mean $\log_{10}$ lake area versus pH interval. Differences in $\log_{10}$ lake area for various pH ranges were tested statistically using the Wilcoxon rank sum test.

To depict reductions in fish species richness associated with lake pH, independent of the effects of lake area, the regression equation for fish species number as a function of lake area was used to calculate the expected number of fish species for each lake in the data set. The mean of the differences between the expected number of fish species and the observed number of fish species (the mean residual) was plotted against pH interval.

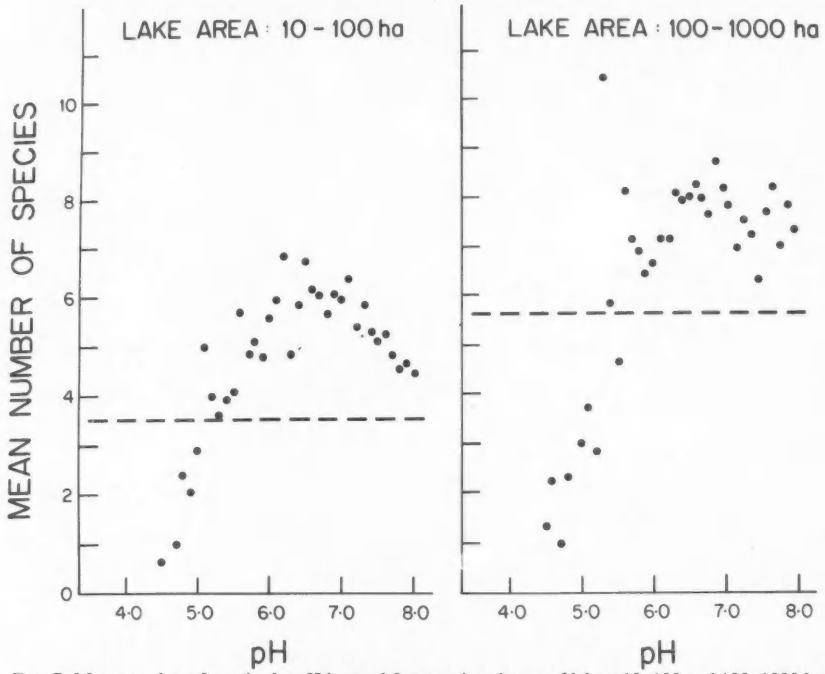

FIG. 7. Mean number of species by pH interval for two size classes of lakes: 10–100 and 100–1000 ha. The broken horizontal lines indicate, at a 2.5% confidence level, the lowest expected number of species predicted from lake size for each area class. The number of lakes per interval for size class 10–100 ha, starting at pH 4.5, is 3, 0, 2, 5, 9, 11 (pH 5.0), 9, 14, 15, 25, 28, 37, 31, 51, 46, 74 (pH 6.0), 55, 66, 77, 58, 51, 54, 40, 43, 34, 34 (pH 7.0), 33, 34, 25, 30, 32, 27, 44, 37, 31, and 31 (pH 8.0). The number of lakes per interval for size class 100–1000 ha, starting at pH 4.5, is 3, 4, 2, 3, 0, 4 (pH 5.0), 7, 6, 2, 6, 6, 8, 17, 22, 17, 34 (pH 6.0), 35, 38, 43, 49, 43, 59, 56, 63, 68 (pH 7.0), 49, 51, 49, 41, 34, 35, 32, 22, 20, and 30 (pH 8.0).

TABLE 3. Results of stepwise multiple regression analyses of $\log_{10}$ (species number + 1) on 19 physical and chemical variables (Table 2) and their $\log_{10}$ transforms. Two data sets were used: all sampled lakes and lakes with pH < 6.0. All variables are significant at the 0.0001 level (type II test).

pH range	Variable	R^2 as each variable added	Sign of coefficient
All values	log lake area	0.18	+
(N = 992)	Total aluminum	0.23	−
	Latitude	0.29	−
	log DOC	0.32	+
	Elevation	0.34	−
pH < 6.0	pH	0.21	+
(N = 272)	Elevation	0.32	−
	log lake area	0.35	+
	log DOC	0.41	+

It was evident from this plot that fish species number declined with pH below 6.0.

Analysis of variance was used to test for a difference in species number between low-pH (<6.0) and high-pH (≥6.0) lakes, after the influence of lake area was removed. The residual species number (number observed minus number predicted by lake area) for each lake was used as the dependent variable in the analysis. The distribution of the species number residuals appeared nearly normal, justifying the use of the significance tests, which are robust with respect to moderate deviations from normality (Miller 1986). Although variances differed between treatments, the larger variance was associated with the larger cell size, making the F-test a conservative estimate of the actual significance of the result (Miller 1986).

For comparison with results from Rago and Wiener (1986), we also employed a nonparametric blocked analysis of variance with observed species number as the dependent variable. The treatments were low pH (<6.0) and high pH (≥6.0), and the data were blocked by lake area to reduce its influence on species number. Block boundaries were set at intervals of 0.1 unit of $\log_{10}$ lake area. The analysis of variance was done on the subset of lakes with $\log_{10}$ area between 0.5 and 2.7 to ensure adequate numbers of lakes in both treatments. This method is useful to test for pH-related effects if no suitable species–area model is available.

Nonparametric blocked analysis of variance was also used to test for a difference in species number between small ($\log_{10}$ lake area <1.5) and large ($\log_{10}$ lake area ≥ 1.5) lakes at similar low pH levels. Species number was the dependent variable and the observations were blocked by intervals of 0.1 pH unit. The pH range 4.9–<5.4 was selected to ensure substantial pH effects and adequate numbers of observations in each cell. The dividing line between small and large lakes was chosen to ensure adequate numbers of observations in each cell and to ensure that the small size class encompassed the range of sizes that Eadie et al. (1986) indicated may be disproportionately affected by acidification compared with larger lakes.

TABLE 4. Spearman correlation coefficients for the regressor variables selected by the stepwise multiple regressions presented in Table 3. *$p \leq 0.0001$.

pH range		Total aluminum	Latitude	DOC	Elevation	pH
All values	Lake area	−0.13*	0.19*	−0.02	−0.14*	0.17*
(N = 992)	Total aluminum		−0.34*	0.14*	0.11	−0.68*
	Latitude			0.29*	0.24*	0.61*
	DOC				−0.30*	0.33*
	Elevation					0.34*
pH < 6.0	Lake area	−0.03	0.33*	−0.22	−0.29*	−0.09
(N = 272)	Total aluminum		0.12	0.27*	−0.12	−0.55*
	Latitude			−0.34*	0.13	−0.07
	DOC				−0.18	0.03
	Elevation					0.12

Stepwise multiple regression analysis was used to identify the physical and chemical variables that influence fish species number and to quantify the relative magnitudes of their effects. Regressions were performed on two sets of data: all lakes and lakes in which it was evident that pH limited fish species richness, i.e. lakes with pH < 6.0. The medians and ranges of the 19 physical and chemical regressor variables are listed in Table 2. In this analysis, we excluded lakes with sulphate values >20 $mg \cdot L^{-1}$ (judged to have received sulphate directly from industrial discharges) and lakes with sodium values >2 $mg \cdot L^{-1}$ (believed to be significantly affected by road salt).

Log_{10} transformations of the regressor variables were included in the regressions along with the original data. Initial regressions with an untransformed dependent variable resulted in increasing residual variance with fish species number. The constancy of the variance was improved by using a log_{10} transformation of fish species number.

Spearman correlation coefficients were used to examine the interrelationships among the selected influential variables. Forced stepwise multiple regressions were used to determine the amount of variation in fish species number, explained by pH, that is independent of other influential factors.

All statistical analyses were performed using the statistical software package SAS (SAS Institute Inc. 1982).

Results

Apparent Changes in Fish Species Number with pH

The mean number of fish species by pH interval decreases steadily below pH 6.4 (Fig. 2). A regression of mean number of fish species on pH interval over the pH range 4.5–6.4 predicts zero species at pH 4.1 after an average decline of about three species per pH unit. Between pH 6.4 and 7.6, mean number of species remains relatively stable at a high level. A slight drop occurs at pH 7.7. This lower level is maintained at higher pH values.

Effects of Lake Area Independent of pH Effects

For lakes with pH ≥ 6.4, larger lakes tend to contain more fish species (Fig. 3). The relationship between mean number of fish species and lake area interval is most linear in the log–log form, with the mean number of fish species increasing by a factor of 1.6 for a 10-fold increase in lake area. The regression of maximum number of fish species on log_{10} lake area (Fig. 4) indicates an increase of about five species for a 10-fold increase in lake size.

Relationship between Lake pH and Lake Area

Over the entire range of pH values, log_{10} lake area and pH are significantly but weakly correlated, with a Spearman correlation coefficient of 0.226 ($p \leq 0.0001$, N = 2913). When the plot of mean log_{10} lake area by pH interval is examined, it is clear that mean log_{10} lake area generally decreases with decreasing pH over the range 5.2 – 6.8 (Fig. 5). However, outside this range the relationship changes. From pH 4.5 to 5.1, mean log_{10} lake area is greater than expected if the trend continued. Several very large values occur for the lowest pH intervals (4.5, 4.6, and 4.7). Log_{10} lake area is relatively constant from pH 6.8 to 7.6, drops at pH 7.7, and then generally decreases with increasing pH at higher pH values. A Wilcoxon rank sum test showed that lakes with intermediate pH values ($6.8 \leq pH < 7.7$) (N = 916) are significantly larger than lakes with lower pH values (pH < 6.8) (N = 1469, $p \leq 0.0001$) and lakes with higher pH values (pH ≥ 7.7) (N = 528, $p \leq 0.0001$). Median log_{10} lake area values for the low, intermediate, and high pH sets of lakes are 1.73, 2.23, and 1.84, respectively.

Effects of Lake pH Independent of Lake Area Effects

The negative effects of pH on fish species number, independent of lake area, are depicted in the plot of mean residual number of species versus pH interval (Fig. 6). The mean residuals decline on either side of a high plateau between pH 6.0 and 7.1. At pH values <6.0 the rate of decline increases with decreasing pH. Between pH 7.2 and 8.0 the mean residuals are generally at a lower level than the values between pH 6.0 and 7.1. Above pH 8.0 the values increase again.

The analysis of variance of the individual lake residuals indicated that the difference between low-pH (<6.0) lakes (N = 492, mean = −0.97) and high-pH (≥6.0) lakes (N = 2421, mean = −0.14) is significant ($p \leq 0.0001$).

The nonparametric analysis of variance of species number by pH class, blocked by log_{10} lake area intervals of 0.1, confirmed that fish species richness is significantly lower at low pH (<6.0), independent of the effects of lake area (N_{low} = 471, N_{high} = 1979, $p \leq 0.0001$).

The nonparametric analysis of variance of species number by lake area class, blocked by pH interval, indicated that there is no significant difference between small (log_{10} area < 1.5) and large (log_{10} area ≥1.5) lakes at relatively low pH levels (4.9 – <5.4) (N_{small} = 54, N_{large} = 44, p = 0.97).

The decline in mean species number with pH below the minimum number predicted by lake area is shown for small (10 – 100 ha) and large (100 – 1000 ha) lakes in Fig. 7. Both small

and large lakes appear to become barren just below pH 4.5. However, because large lakes contain more species at high pH ($\geq$6.0) than small lakes, the decline in species richness is greater for these lakes.

Lake pH varies in concert with a number of other chemical variables. For those lakes in the data set with complete chemistry data ($N = 992$), the correlates of pH include alkalinity ($r = 0.94$), calcium ($r = 0.85$), magnesium ($r = 0.86$), conductivity ($r = 0.83$), total aluminum ($r = -0.64$), and manganese ($r = -0.51$). For the subset of lakes with pH < 6.0 ($N = 272$), the correlates of pH include alkalinity ($r = 0.80$), total aluminum ($r = -0.55$), and manganese ($r = -0.36$). All correlations are expressed as Spearman coefficients and are significant at the 0.0001 level.

Relative Magnitudes of the Effects of Lake Area and Lake pH on Fish Species Number

When all sampled lakes with a complete parameter set were included in a stepwise multiple regression analysis, $\log_{10}$ lake area was selected as the dominant factor, explaining 18% of the variance in species number (Table 3). The remaining four minor factors, total aluminum, latitude, $\log_{10}$ dissolved organic carbon, and elevation, explained a further 16% of the variance. The signs of the regression coefficients for these variables indicate positive effects on fish species richness by lake size and dissolved organic carbon and negative effects by total aluminum, latitude, and elevation. The interrelationships among the variables are weak, although significant (Table 4). pH was not selected as a significant factor but is represented by its correlate, total aluminum.

When a stepwise regression was performed on the set of lakes with pH < 6.0, pH was selected as the dominant factor, explaining 21% of the variation in fish species number (Table 3). Elevation explained an additional 11% of the variance. The remaining two factors, $\log_{10}$ lake area and $\log_{10}$ dissolved organic carbon, together explained a further 9%. The positive regression coefficient for pH reflects the negative effect of decreasing pH on fish species number. The signs of the regression coefficients of the other factors agree with those in the previous regression using all sampled lakes.

Forced stepwise regressions were used to control the entry of pH into the regression relative to other influencing factors. When all sampled lakes with pH and lake area values were considered ($N = 2798$), $\log_{10}$ lake area alone explained 28% of the variation in fish species number. The addition of pH only explained a further 1% of the variation. However, when the subset of lakes with pH < 6.0 was considered ($N = 447$), $\log_{10}$ lake area alone explained 6.1% of the variation. The addition of pH explained another 21.8%. Even when elevation, $\log_{10}$ lake area, and $\log_{10}$ dissolved organic carbon were entered first, explaining 25.8% of the variation in fish species number in lakes with pH < 6.0 ($N = 286$), the addition of pH explained a further 15.9% of the variation.

Discussion

Species Richness and Lake Area

Lake size is the dominant abiotic factor we found influencing fish species richness in Ontario lakes. In stepwise multiple regression analysis, lake area explained 18% of the variation in species richness, compared with 5% for total aluminum, 6% for latitude, 3% for dissolved organic carbon, and 2% for elevation (Table 3). Although there is some intercorrelation among the independent variables in the multiple regression, which might reduce the apparent effects of minor factors, it seems unlikely that any of these factors can match the influence of lake area on fish species number. Therefore, any studies of the influence of potential factors on species number in Ontario lakes must consider and account for the effects of lake area. This has been done by Somers and Harvey (1984) and Harvey and Lee (1982), who estimated the effects of acidification on fish species in the Wawa and La Cloche regions of Ontario, respectively, by first using lake area to predict the expected number of fish species.

Our species number – lake area relationship may be largely a species number – habitat diversity model. Habitat diversity is an important factor in determining fish species richness in lakes (Wiener et al. 1984; Keast 1978; Eadie and Keast 1984). Furthermore, habitat diversity can be associated with lake size. Cool, well-oxygenated water or wave-washed, hard-bottomed substrates are generally limited or absent from small lakes and thereby exclude species that require these habitats (Rahel 1986). Vegetation diversity and substrate/vegetation diversity are related to fish species richness in Wisconsin lakes and are significantly correlated with lake area (Tonn and Magnuson 1982). Eadie et al. (1986) considered three mechanisms that may account for the relationship between species number and lake area: habitat diversity (Williams 1964); species immigration and extinction (MacArthur and Wilson 1967); and passive species sampling (Connor and McCoy 1979). They concluded that the most probable factor was habitat diversity. A tempting hypothesis to explain the species number – lake area relationship is that larger lakes generally occur at lower elevations than smaller lakes and are therefore accessible to larger numbers of species. However, within the high-pH ($\geq$6.4) data set that was used to develop our species number – lake area relationship, lake area and elevation are unrelated (Spearman correlation coefficient $r = 0.07$, $p = 0.0025$, $N = 1951$).

A number of previous studies have produced values for the slope of the fish species number – lake area line: 0.29 for 12 lakes in Wisconsin (Tonn and Magnuson 1982); 0.26 for 12 lakes in New York (Browne 1981); 0.21 for 82 lakes in Ontario (Eadie et al. 1986); and 0.16 for 14 large North American lakes (Barbour and Brown 1974). Although Barbour and Brown (1974) found a relatively small slope, the low value is likely due to the effects of latitude. Two large lakes in the far north (61 and 66°N) appear to be very influential in reducing the slope of their regression line. Eadie et al. (1986) found that their slope for 82 Ontario lakes increased from 0.21 to 0.24 when the effects of latitude were statistically controlled. In our data set (pH $\geq$ 6.4), latitude is weakly correlated with the lake area (Spearman $r = 0.16$, $p \leq 0.0001$, $N = 1951$) and therefore unlikely to have much effect on the slope of our species number – lake area line. Spearman correlations of lake area with other variables that were found to influence species number are all very weak: $r = 0.07$ with elevation ($p = 0.0025$, $N = 1951$); $r = -0.07$ with pH ($p = 0.0025$, $N = 1934$); $r = 0.18$ with total aluminum ($p \leq 0.0001$, $N = 827$); and $r = 0.02$ with dissolved organic carbon (DOC) ($p = 0.59$, $N = 695$). Our slope (0.20) is lower than most values found for fish species number – lake area relationships, but within the range 0.20–0.35 found by MacArthur and Wilson (1967) for species–area relationships for islands. Connor and McCoy (1979), in an analysis of 90 species–area relationships, found that the mean slope was 0.31, with a standard deviation of 0.227.

Rahel (1986) found that alkalinity affected the slope of the species number – lake area relationship in Wisconsin lakes. The slope for low-alkalinity lakes ($\leq$10 mg·L^{-1} as $CaCO_3$) was significantly lower than for high-alkalinity lakes (>10 mg·L^{-1} as $CaCO_3$). However, one large lake with pH 5.6 appears to have been very influential in lowering the slope of the line for the low-alkalinity lakes. When we analyzed Ontario lakes with pH $\geq$ 6.4, we found no significant difference in slopes between low- and high-alkalinity lakes (N_{low} = 671, N_{high} = 1263, p = 0.37). Rahel found that when both low- and high-alkalinity lakes were present in his data set, lake area explained 50% of the variation in species number and alkalinity a further 8%. However, we found that when low-pH (<6.4) lakes were removed and both low- and high-alkalinity lakes were present, lake area explained 32% of the variation in species number and alkalinity only a further 1% ($p \leq 0.0001$, N = 1890). The sign of the regression coefficient for alkalinity was negative, not positive as Rahel (1986) had found.

Maximum species richness is strongly related to lake size in Ontario lakes. The potential number of fish species in a lake of a given size, under the most favorable abiotic and biotic conditions, can be predicted from the equation in Fig. 4. This relationship may be useful to resource managers by setting upper limits on species richness when lakes are being considered for habitat enhancement, water quality improvement, and stocking. Complex community types, composed of many species, may not be possible in small lakes due to the size-related ceiling on fish species number. Assuming that lake area is mainly an index of habitat diversity, it appears that in small lakes the number and/or size of distinct habitat types is restricted in such a way as to limit the number of species possible.

Lake Area and pH

Lake size decreases with pH in Ontario lakes, as it does in Wisconsin lakes (Rago and Wiener 1986), but not over the entire range of pH values. The decrease begins at pH 6.7, well above the pH values (<6.0) at which the limiting effects of pH and pH-related factors become evident. Therefore, in a simple plot of mean species number versus pH (Fig. 2), the initial decline in species number is mainly due to decreasing lake area. At lower pH values (<6.0) the effects of pH increase in importance and eventually dominate the effects of lake area. At pH values <5.2, even the very large size of lakes (Fig. 5) does not noticeably disrupt the steady decline in species number with pH (Fig. 2). Within our data set, the relatively large mean $\log_{10}$ lake area values at pH < 5.2 are due to an increasing proportion of large acidified lakes near Sudbury, Ontario. For example, all the lakes in the two pH intervals with the largest mean $\log_{10}$ lake areas (pH 4.6 and 4.7) are near Sudbury and appear to have been highly impacted by the SO_2 emissions originating from the smelting operations in Sudbury (Keller and Pitblado 1985).

At the high end of the pH range ($\geq$7.7), lake size was found to decrease with increasing pH (Fig. 5). Since high-pH lakes tend to be smaller than circumneutral (pH 6.8 – 7.6) lakes, lake area may be responsible for the drop in species richness in high-pH lakes (Fig. 2). Factors other than lake area appear to favour increasing fish species number with pH (Fig. 6) and actually moderate the decline in species number in high-pH lakes (Fig. 2).

Species Number and pH

When the effects of lake size were taken into account, a decline in species number with pH was apparent below pH 6.0. The adverse effects of acidic water on many fish species have been documented both in the field and laboratory (Haines 1981; Magnuson et al. 1984). Summaries of information on fish species distribution with respect to pH (Eilers et al. 1984; Magnuson et al. 1984; Wales and Beggs 1986) suggest that species richness can begin to decline noticeably at or about pH 6.0 and that lakes will likely be barren of fish below approximately pH 4.0. Even though the exact nature of the species number – pH relationship may vary among regions according to the fish species assemblages present, our results agree well with what is predicted by individual species' sensitivities. The empirically derived relationship between species number and pH, however, does not imply that a simple, direct cause and effect relationship exists between pH and species number. pH is often correlated with other chemical variables such as aluminum and calcium and acts concurrently and synergistically with these to affect the health and development of fish (Wright and Snekvik 1978; McDonald et al. 1980; Muniz and Leivestad 1980; Baker 1982).

In our data set the differences between observed species number and that predicted by lake area are relatively small down to pH 5.1. For example, at pH 5.2 the mean difference is 1.8 species (Fig. 6), which may seem inconsequential. However, since the mean size of lakes decreases with pH, the number of species predicted by lake size is also relatively small. At pH 5.2 the mean $\log_{10}$ lake area is 1.36 (Fig. 5) and the predicted number of species is 4.8. Thus a mean loss of 1.8 species due to pH effects represents an average drop of 38% in species richness. The loss of only one or two species due to low pH can significantly reduce the species richness of the relatively simple communities found in small lakes. If population stability is associated with community complexity, then the populations surviving at low pH should be less stable and therefore more susceptible to stresses such as exploitation, eutrophication, and species introductions.

Species Richness and Other Abiotic Factors

Latitude, elevation, total aluminum, and dissolved organic carbon explained significant amounts of variation in species number in Ontario lakes. Latitude is most likely an index of climatic factors with more extreme climatic conditions at higher latitudes. For example, climatic factors have been shown to limit the northern distribution of smallmouth bass in Ontario (Shuter et al. 1980). Isolation from potential colonizing species may also be partly responsible for the negative effects of latitude on species richness (Eadie et al. 1984). Barbour and Brown (1974) found that latitude can be a major factor influencing species number. Latitude explained 64% of the variation in species number in their set of 14 North American lakes. The reduced importance of latitude in our Ontario lake set is likely due to the smaller range of latitudes spanned by our lakes. Furthermore, within our subset of low-pH lakes (<6.0), with an even smaller range of latitudes (Table 2), latitude was not selected as a significant factor in the multiple regression analysis. Latitude appears to be partly responsible for the deviations of observed species number from expected species number, predicted from lake area, in high-pH ($\geq$6.0) lakes (Fig. 6). Lakes with lower than expected species numbers (pH 7.2 – 8.0) have a higher median latitude (48.6°, N = 772) than lakes with generally higher species numbers (pH 6.2 – 6.9; 45.9°, N = 986).

Elevation effects on species richness may be due to increased isolation at higher altitudes. There is a weak negative correlation between elevation and lake area in low-pH (<6.0) lakes

(Table 3), which may partly account for the relatively large variation in species number (10.9%) explained by elevation. In the set of lakes spanning the entire pH range, elevation explained a small but significant portion of the residual variation in species number even though it entered after all the other influencing factors. Therefore, there are elevation effects on species number that cannot be explained by the possibilities that lakes at higher elevations are smaller, more acidic, or further north. Elevation may be partly responsible for the relatively high number of species in very high pH lakes (pH 8.3 – 8.6), after the effects of lake size are removed (Fig. 6). The median elevation of these lakes (274 m, $N = 97$) is lower than lakes with pH 7.2 – 8.0 (336 m, $N = 272$) and lakes with pH 6.2 – 6.9 (380 m, $N = 986$).

Aluminum and dissolved organic carbon exhibited opposite effects on species richness. The adverse effects of high concentrations of inorganic aluminum on fish have been documented in numerous field and laboratory studies (Baker 1982). However, in lakes with sufficient levels of dissolved organic carbon, aluminum in the water can complex with the available organic ligands and produce a harmless organically bound form instead of the toxic inorganic monomeric form (Baker 1982).

A substantial portion of the variation in species richness remains unexplained. Although stochastic events (e.g. storms, epizootics) and sampling error may account for a large part of this unexplained variation, an enhanced set of factors should improve our predictive capability. For example, if lake area is mainly a rough index of habitat diversity, then it could be replaced by a set of factors that describe available habitat types in more detail (e.g. substrate types, vegetation types, oxygen regime, temperature regime, etc.). In addition to abiotic factors, biotic factors such as the presence of predator species could be included (Tonn and Magnuson 1982; Rahel and Magnuson 1983). With improved predictive capabilities, the magnitude and extent of the effects of anthropogenic stresses such as acidification can be more accurately described.

Of our set of 19 physical and chemical factors, lake area was the dominant factor influencing fish species richness in Ontario lakes. pH and pH-related factors (e.g. aluminum) can have substantial effects at pH values less than 6.0, overwhelming the effects of lake area in very low pH lakes. Latitude, elevation, and dissolved organic carbon have significant but less dramatic effects on species richness. In total, these abiotic factors explained 34% of the variation in fish species richness in the 992 lakes with complete physical and chemical data.

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Growth and Feeding Responses of Male versus Female Yellow Perch (*Perca flavescens*) Treated with Estradiol-17β

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In yellow perch (*Perca flavescens*) (initially 13–16 g total weight) fed to satiation (3.0–3.5% of body weight per day), estradiol-17β (E_2) at 15μg/g diet stimulated weight gain and food consumption of both sexes but did not influence food conversion efficiency (FCE), as measured by weight gain of fish per weight of food consumed. Females fed to satiation gained more weight, consumed more food, and had higher FCE than males. In perch fed a restricted ration (1.2% of body weight per day), the differences between the sexes in weight gain were reduced and due entirely to differences in FCE, and weight gain was not improved by E_2. Spatial segregation or integration of the sexes had no influence on sex-related growth patterns in perch fed either the satiation or restricted ration. Carcass composition of perch treated for 84 d with E_2 at 2, 20, or 50 μg/g diet did not differ from that of controls. These data indicate that (1) estrogens promote growth in yellow perch by stimulating food consumption, (2) female perch outgrow males because of both greater food consumption and higher FCE, and (3) growth differences between the sexes are not a consequence of intersexual competition for food.

L'étude consistait à administrer de l'oestradiol-17β (E_2) à une dose de 15 μg/g dans le régime alimentaire de perchaudes (*Perca flavescens*) (poids total initial 13–16 g) nourries à satiété (3,0–3,5 % du poids corporel par jour); on a observé une stimulation du gain de poids et de l'ingestion de nourriture chez les perchaudes des deux sexes, mais le traitement est resté sans effet sur l'efficacité de conversion alimentaire (ECA), mesurée par le rapport du gain corporel du poisson au poids de nourriture ingérée. Le gain de poids, l'ingestion de nourriture et l'ECA étaient plus élevés chez les femelles nourries à satiété que chez les mâles. Chez les perchaudes recevant une ration limitée (1,2 % du poids corporel par jour), les différences de gain de poids entre les deux sexes étaient atténuées et portaient entièrement sur l'ECA; le gain de poids n'a pas été amélioré par le traitement à l'E_2. La ségrégation ou l'intégration spatiales des deux sexes est restée sans effet sur les types de croissance liées au sexe dans le cas des perchaudes nourries à satiété ou recevant une ration limitée. La composition des carcasses de perchaudes traitées pendant 84 d à l'E_2, à la dose de 2, 20 ou 50 μg/g d'aliments ne présentaient aucune différence par rapport à celles de perchaudes témoins. Ces données révèlent les éléments suivants : 1) les œstrogènes favorisent la croissance des perchaudes en stimulant l'ingestion de nourriture, 2) la croissance des perchaudes femelles est supérieure à celle des mâles en raison d'une plus grande ingestion de nourriture et d'une ECA plus élevée, et 3) les différences de croissance entre les deux sexes ne résultent pas d'une compétition pour la nourriture.

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The potential of improving fish growth by steroid hormone treatment has been examined in several teleost species (see reviews by Donaldson et al. 1979; Higgs et al. 1982; McBride et al. 1982). In most of these fishes, androgens, but not estrogens, are effective growth promoters (Donaldson et al. 1979). Androgen-induced growth improvements were due primarily to increased food conversion efficiency (FCE) in coho salmon (*Oncorhynchus kisutch*) (Fagerlund et al. 1979; Yu et al. 1979; McBride et al. 1982), rainbow trout (*Salmo gairdneri*) (Matty and Cheema 1978; Ince et al. 1982), and carp (*Cyprinus carpio*) (Lone and Matty 1980, 1982). The effect of androgens on food consumption apparently varies between species. These steroids increased food consumption in coho (McBride et al. 1982; Fagerlund et al. 1983) and chinook salmon (*Oncorhynchus tshawytscha*) (Schreck and Fowler 1982), but had either negligible (Matty and Cheema 1978) or negative (Ince et al. 1982) effects on food consumption in rainbow trout.

Studies by Cowey et al. (1973) on plaice (*Pleuronectes platessa*) and by our group (Malison et al. 1985) on yellow perch (*Perca flavescens*) indicate that estrogenic compounds stimulate growth in at least some fish species. Diethylstilbestrol improved the growth of plaice by increasing both food consumption and FCE (Cowey et al. 1973). The manner by which estradiol-17β (E_2) improves growth of perch has not been previously reported.

In addition to affecting overall growth, steroid treatment may induce metabolic changes that alter carcass composition. Coho salmon treated with 17α-methyltestosterone had an increased percentage of carcass protein and variable carcass lipid and moisture contents (Higgs et al. 1982). In androgen-treated carp, Lone and Matty (1980) reported increased percentages of protein and lipid in muscle and decreased whole-carcass moisture content.

The fact that exogenous steroids can exert such effects on the growth and metabolism of fish suggests that endogenous steroids influence these processes and may mediate the sexually

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related differences in growth and adult size that are characteristic of many fish species, including yellow perch (Scott and Crossman 1973; Schott 1980). Sexually related dimorphic growth could result from several factors (e.g. genetic, physiological, or behavioral), including differences in food consumption, FCE, or competition for food. The following experiments were designed to determine in perch (1) the difference between the sexes in and the effect of E_2 on growth, food consumption, and FCE, (2) the effect of intersexual competition on growth, and (3) the effect of E_2 on carcass composition.

Materials and Methods

General Procedures

Methods of procuring and rearing yellow perch in our laboratory have been described previously (Malison et al. 1985). Prior to each experiment, fish were assigned and acclimatized to 110-L round fiberglass tanks (61.0-cm diameter × 50.5-cm depth, with 2 L/min flow) for at least 1 wk under environmental conditions optimal for perch growth (21 ± 1°C, 16-h light : 8-h dark photoperiod, see Huh et al. 1976). Steroids (E_2 or cholesterol (C)) were added to the food (Silver Cup salmon food, Sterling H. Nelson and Sons, Inc., Murray, UT 84107) as detailed by Malison et al. (1986). Control diets were treated with cholesterol following studies (Malison et al. 1985) which demonstrated that this steroid, at the level added, has no influence on perch growth (Malison et al. 1985).

Sex determinations (when necessary) were made prior to assignment of fish to experimental tanks. To accomplish this, age 0 perch were overwintered under ambient environmental conditions, and by the following spawning season (April), semen could be expressed from many males when pressure was applied to the abdomen. We used this characteristic in combination with a technique developed in our laboratory (unpubl. data) that relies on morphological differences between the sexes in the urogenital–anal area. Perch whose sex could not be clearly distinguished were not used. Autopsies after experiments indicated that our sex determinations had been 100% accurate.

Experiment 1

Twenty-four fish of 13–16 g each were randomly assigned to each of 32 tanks (four tanks per treatment). The experiment was of 2^3 factorial design, the factors being (1) sex, male or female, (2) ration, fish fed either to satiation (3.0–3.5% of body weight per day) or a restricted amount of food (1.2% of body weight per day), and (3) steroid, either E_2 or C, added to the diet at a level of 15 μg/g. The level of feeding for the restricted ration was chosen at 1.2% of body weight per day because at this level, fish remained hungry at all times but continued to grow. The amount of food given to fish fed the restricted ration was adjusted weekly to correspond with the actual (on days 0, 14, 28, and 42) or estimated (on days 7, 21, 35, and 49) weight of fish in each tank. The dosage of E_2 was selected at 15μg/g diet because it is near optimal in promoting growth (Malison et al. 1985).

Perch feeding behavior is readily disturbed by human activity and movement. To minimize such disturbance, the experimental tanks were enclosed in chambers (four tanks per chamber) equipped with viewing ports made of one-way glass. With this arrangement, feeding could be carefully monitored and a satiation ration could be closely approximated. All fish were fed twice daily by hand beginning at approximately 0730 and 1630. At each feeding the diet was delivered slowly to each tank over two 1.5-min intervals. These intervals were separated by an hour during which fish were not fed. Consumption by the fish in each tank at each feeding was recorded. In tanks fed the satiation rate, only a small amount of food (<1% of the total) remained uneaten after each feeding; this amount was not corrected for. We are confident that these feeding procedures resulted in a close approximation of a satiation ration because the growth rates observed were near the theoretical upper limit for perch (Kitchell et al. 1977) and were similar to those of perch that are routinely fed to excess several times daily in our laboratory.

TABLE 1. Design of experiment 2.

Arrangement of sexes within tanks[a]	Ration[b]	
	Satiation	Restricted
Sexually segregated	M F	M F
Sexually integrated	M and F	M and F

[a]There were four tanks per treatment group for a total of 24 tanks. Each tank contained 24 males (M), 24 females (F), or 12 males and 12 females (M and F). Fish of different sexes in integrated tanks were fin-clipped for identification.

[b]Fish were fed either to satiation or a restricted amount of food (see Materials and Methods, experiment 1, for details).

The fish in each tank were counted and weighed collectively on days 0, 14, 28, 42, and 56 of treatment. For this experiment, mean gain in total weight was used as a measure of growth and weight gain of fish per weight of food consumed as a measure of FCE. Previous studies have shown that, in perch, estrogen promotes overall body growth (both weight and length), does not alter condition factor, and does not induce significant gonadal growth under the environmental conditions used (Malison et al. 1985, 1986). Mean gain in total weight and FCE were examined by three-way (sex × ration × steroid) ANOVA. Mean food consumption by fish fed to satiation was examined by two-way (sex × steroid) ANOVA.

Experiment 2

Experiment 2 was conducted at the same time and under similar conditions as experiment 1. The experimental design is outlined in Table 1. All fish of a given sex in each tank were weighed collectively on days 0, 14, 28, 42, and 56 of treatment. For sexually segregated fish, mean gain in total weight was examined by two-way (sex × ration) ANOVA with four tanks per treatment. For sexually integrated fish, the difference in mean weight gain between the sexes was analyzed using a *t*-test for paired observations (Steel and Torrie 1960). To examine the effect of the satiation versus the restricted ration in sexually integrated fish, the difference in mean weight gain between females (F) and males (M) in each tank was considered a variable (F − M), with $N = 4$ groups of fish per ration. The difference in F − M between the satiation and restricted rations was analyzed using a *t*-test. In order to examine the difference between sexually segregated and sexually integrated fish, differences between F − M of integrated fish and the weight gain of segregated females minus the weight gain of segregated males were analyzed by a separate *t*-test for each ration, according to

the method of Steel and Torrie (1960) for comparing samples from populations with unequal variances.

Experiment 3

Two size-groups of fish (initial total weight = 0.5–0.7 or 8–12 g and final total weight = 12–20 or 25–45 g, respectively) were treated for 84 d with C at 50 μg/g diet or E_2 at 2, 20, or 50 μg/g diet (four tanks per treatment). Growth rates of fish in this experiment have been previously reported (Malison et al. 1985). After final weight and length measurements were taken, 10 fish from each tank were killed and their intestinal contents were removed. The carcasses were individually weighed, pooled for each tank, and homogenized in a Waring blender. Samples of the homogenates were dried, and weight loss over a 24-h period in an oven at 80°C was used as a measure of moisture content. Dried samples were ground using a mortar and pestle, and total organic nitrogen content of these samples was determined using a semi-micro Kjeldahl procedure for digestion (AOAC 1980) and a colorimetric phenol–hypochlorite reaction (Weatherburn 1967). Total lipid and ash contents were determined using the Bligh and Dyer (1959) and AOAC (1980) procedures, respectively. Percent moisture, protein, lipid, and ash for each size-group of fish were examined by separate ANOVAs.

Results

Experiment 1

Data on weight gain in Fig. 1 and Table 2 indicate that (1) females grew faster than males, and this difference was greater among fish fed to satiation than among those fed a restricted ration (significance by ANOVA of "sex" and "sex × ration," see Table 3), (2) E_2 improved growth of fish fed to satiation, but retarded growth of fish fed a restricted ration (significance of "steroid" and "steroid × ration"), and (3) E_2 improved growth of females more than males among fish fed to satiation (significance of "sex × steroid" and "sex × steroid × ration"). Among fish fed to satiation, females consumed more than males, and E_2 increased food consumption of both sexes of fish (significance of "sex" and "steroid," see Tables 2 and 3). Data on FCE in Table 2 indicate that (1) for all treatments, females had higher FCEs than males (significance of "sex"), (2) E_2 had no effect on FCE of fish fed to satiation, but had a negative effect on FCE of fish fed a restricted ration (significance of "steroid" and "steroid × ration"), and (3) fish fed a restricted ration had higher FCEs than fish fed to satiation (significance of "ration").

Experiment 2

Regardless of whether fish were segregated or integrated by sex, females gained more weight than males, and this difference was greater among perch fed to satiation than among those fed the restricted ration (Table 4). Segregation or integration of the sexes did not significantly influence the growth differences between the sexes, regardless of ration.

Experiment 3

Fish (of either size group) treated with C at 50 μg/g diet or E_2 at 2, 20, or 50 μg/g diet did not differ in any measured component of carcass composition (Table 5).

Discussion

Our findings demonstrate that E_2 promotes growth in yellow perch by stimulating food consumption (appetite) but not by affecting FCE (see Tables 2 and 3). In this regard, the manner

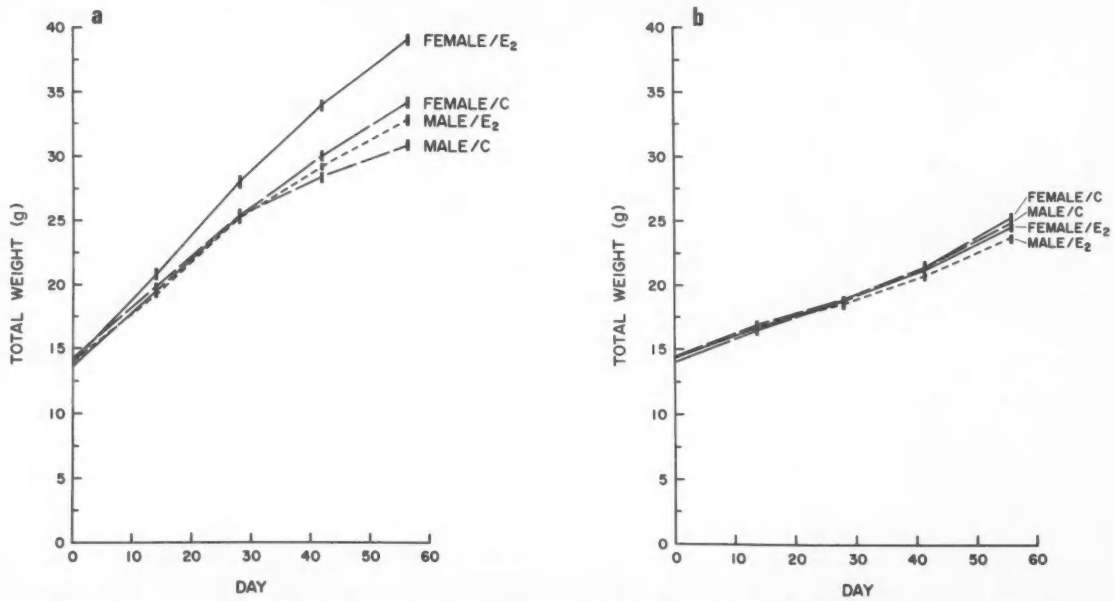

FIG. 1. Effect of E_2 or C on weight gain of male and female yellow perch fed (a) to satiation (3.0–3.5% of body weight per day) or (b) a restricted amount of food (1.2% of body weight per day). Each bar represents the mean ± SE of the fish from four tanks (24 fish per tank). See Table 3 for results of ANOVAs.

TABLE 2. Weight gain, food consumption, and FCE (as measured by weight gain of fish per weight of food consumed) of male (M) and female (F) yellow perch fed to satiation (S, 3.0–3.5% of body weight per day) or a restricted (R, 1.2% of body weight per day) ration, treated with E_2 or C at 15 μg/g diet. Data represent mean ± SE, $N = 4$ tanks of fish per treatment.[a]

Sex	Steroid	Ration	Weight gain (g)	Food consumption (g)	FCE
M	C	S	16.66 ± 0.19	19.85 ± 0.33	0.84 ± 0.03
M	E_2	S	18.92 ± 0.37	22.86 ± 0.24	0.83 ± 0.02
F	C	S	20.63 ± 0.45	22.31 ± 0.33	0.93 ± 0.02
F	E_2	S	25.20 ± 0.57	26.76 ± 0.62	0.94 ± 0.02
M	C	R	10.28 ± 0.17	11.00 ± 0.07	0.93 ± 0.02
M	E_2	R	9.23 ± 0.22	10.98 ± 0.03	0.83 ± 0.02
F	C	R	11.10 ± 0.09	11.04 ± 0.05	1.00 ± 0.00
F	E_2	R	10.24 ± 0.12	11.26 ± 0.18	0.90 ± 0.02

[a]Fish weighed 13–16 g at the start of treatment, and the treatment period was 56 d. See Table 3 for results of ANOVAs.

TABLE 3. Results of ANOVAs for experiment 1.

Source of variance[a]	df[b]	Level of significance[c]		
		Weight gain	Food consumption	FCE[d]
Total	31 (15)	—	—	—
Sex (X)	1 (1)	$P < 0.01$	$P < 0.01$	$P < 0.01$
Steroid (Y)	1 (1)	$P < 0.01$	$P < 0.01$	$P < 0.01$
Ration (Z)	1	$P < 0.01$	—	$P < 0.01$
$X \times Y$	1 (1)	$P < 0.01$	NS	NS
$X \times Z$	1	$P < 0.01$	—	NS
$Y \times Z$	1	$P < 0.01$	—	$P < 0.01$
$X \times Y \times Z$	1	$P < 0.05$	—	NS
Error	24 (12)	—	—	—

[a]Main effects were (1) "sex," male or female, (2) "steroid," C or E_2 at 15 μg/g diet, and (3) "ration," fish were fed either to satiation or a restricted amount of food. See Materials and Methods for details.

[b]Numbers outside parentheses are the degrees of freedom (df) for the ANOVAs on weight gain and FCE; numbers within parentheses are the df for food consumption.

[c]P values are for means at the end of the 56-d treatment period. ANOVA on food consumption was done only for groups of fish fed to satiation.

[d]FCE = food conversion efficiency as measured by weight gain of fish per weight of food consumed.

TABLE 4. Effect of spatial segregation (Seg) versus integration (Int) on weight gain of male (M) and female (F) yellow perch fed to satiation (S, 3.0–3.5% of body weight per day) or a restricted (R, 1.2% of body weight per day) ration. Data represent mean ± SE, $N = 4$ groups of fish per treatment.[a]

Sex	Arrangement of sexes within tanks	Ration	Weight gain (g)
M	Seg	S	16.66 ± 0.19
M	Int	S	15.03 ± 1.33
F	Seg	S	20.63 ± 0.45
F	Int	S	21.33 ± 0.94
M	Seg	R	10.28 ± 0.17
M	Int	R	10.87 ± 0.74
F	Seg	R	11.10 ± 0.09
F	Int	R	12.15 ± 0.47

[a]Each observation was the mean of all fish of one sex in one tank (24 fish for segregated tanks or 12 fish for integrated tanks) and represents the total weight gain for the entire 56-d treatment period. ANOVA for segregated fish showed "sex," "ration," and "sex × ration" significant at $P < 0.01$. t-tests revealed (1) differences ($P < 0.05$) between the sexes and between the rations for sexually integrated fish and (2) no difference between segregated and integrated fish fed either ration.

by which E_2 enhances perch growth apparently differs from the manner by which steroids or their analogs stimulate growth in other teleosts. For example, Cowey et al. (1973) found that diethylstilbestrol promoted growth in plaice partly through an increase in FCE, and studies on carp and various salmonids have shown that androgens promote growth in these fishes *primarily* by improving FCE (Matty and Cheema 1978; Fagerlund et al. 1979; Lone and Matty 1980, 1982).

TABLE 5. Carcass composition of two size-groups of yellow perch treated with E_2 or C for 84 d. Data represent mean ± SE, $N = 4$ tanks per treatment.

Fish size[a]	Steroid	Dose (μg/g diet)	Carcass composition[b]			
			Moisture (%)	Protein (%)	Lipid (%)	Ash (%)
Sm	C	50	73.50 ± 0.58	15.70 ± 0.20	6.37 ± 0.05	3.30 ± 0.05
Sm	E_2	2	72.90 ± 0.59	16.56 ± 0.45	6.50 ± 0.30	3.33 ± 0.12
Sm	E_2	20	74.05 ± 1.05	15.93 ± 0.59	6.13 ± 0.23	3.24 ± 0.14
Sm	E_2	50	74.50 ± 0.56	15.85 ± 0.33	6.27 ± 0.14	3.26 ± 0.07
Lg	C	50	72.15 ± 0.31	17.64 ± 0.30	6.05 ± 0.21	3.92 ± 0.05
Lg	E_2	2	71.73 ± 0.34	17.84 ± 0.43	6.22 ± 0.27	3.80 ± 0.11
Lg	E_2	20	72.22 ± 0.27	17.77 ± 0.38	6.45 ± 0.08	3.65 ± 0.10
Lg	E_2	50	71.66 ± 0.18	18.63 ± 0.86	6.44 ± 0.10	3.96 ± 0.17

[a]Size ranges of fish on days 0 and 84 were 0.5–0.7 and 12–20 g, respectively, for small (Sm) fish and 7–10 and 25–45 g, respectively, for large (Lg) fish.

[b]Compositions of entire fish were analyzed following removal of intestinal contents. There were no differences between treatments within each size-group of fish.

Although E_2 did not promote perch growth by improving FCE, the fact that E_2 treatment impaired growth and FCE in fish fed a restricted ration (Table 2) indicates that E_2 can influence perch growth by means other than through food consumption. One well-studied effect of estrogen in most oviparous animals is its stimulation of hepatic vitellogenin synthesis (Wallace 1978), a process requiring substantial amounts of protein and energy. Unpublished studies conducted in our laboratory have shown that E_2 stimulates this process in both sexes of perch. Vitellogenin is not physiologically useful in males, and in experiment 1 it was not used to any great extent by females. The latter can be inferred because the ovarian weights of fish in this study were not more than 2% of the total body weight. In experiment 1, the net result of vitellogenin synthesis induced by E_2 may have been to reduce the amount of protein and energy available for overall body growth, thereby decreasing FCE in E_2-treated fish. Such an effect may have been small enough to be detectable only in slow-growing fish fed a restricted ration.

One surprising result of our studies was that carcass composition of yellow perch was not altered by E_2 treatment over a wide range of dosages (one dose was too low to promote growth, one dose promoted growth, and one dose was high enough to impair growth; see Malison et al. 1985). It is generally accepted that sex steroids in most vertebrates induce metabolic changes that influence body composition. In salmonids, androgens decrease the percentages of body fat, visceral fat, and muscle moisture, and increase the percentages of muscle fat and protein (Higgs et al. 1982). In rats and ruminants, estrogens and compounds with estrogen-like activity lower the percentage of body fat (Hafs et al. 1971; Gray and Wade 1981; Ramirez 1981). In the golden shiner (*Notemigonus crysoleucas*), de Vlaming et al. (1977) found that E_2 had either a positive or negative effect on the percentage of body fat, depending on dose, photoperiod, and sex. Our results suggest that estrogens do not influence carcass composition in perch, at least under the conditions used in our studies (i.e. conditions optimal for growth).

Among perch fed to satiation, E_2 improved the growth of females more than males. Estrogen promoted growth in females as soon as treatment had begun, but did not promote growth in males until after 1 mo of treatment (Fig. 1a). One explanation for this result is that E_2 target tissue(s) involved in growth stimulation may first need to be primed by E_2 in order to respond to subsequent E_2 treatment. Tissues in the females (but not the males) in experiment 1 were probably exposed to significant quantities of endogenous E_2 prior to treatment. Such a priming mechanism apparently functions in the liver of amphibians; hepatic cells (in vivo and in vitro) respond more rapidly to E_2 (by producing vitellogenin) if they have been previously treated with this hormone (Clemens 1974; Stanchfield and Yager 1978; Westley and Knowland 1979). The latter authors suggested that E_2 priming of hepatic cells induces the synthesis of intracellular estrogen receptors, making the cells more responsive to subsequent E_2 treatment.

Our finding that C-treated perch fed a restricted ration had higher FCEs than those fed to satiation (Table 2) supports the model outlined by Brett and Groves (1979), which states that FCE is optimized at a submaximal ration level. Such results have been attributed to increased assimilation of nutrients by the gut in fish fed a restricted ration (discussed by Kapoor et al. 1975) or to higher metabolic costs in heavily fed fish (Brett and Groves 1979). It is highly unlikely that the differences in FCE that we measured could have been due to the small amount of food (<1% of the total; see Materials and Methods) that was not consumed by fish fed to satiation.

The findings that females consumed more food than males and that E_2 stimulated food consumption (Tables 2 and 3) provide additional support for our hypothesis that E_2 (partially) mediates sexually related dimorphic growth in perch (Malison et al. 1985). Howver, E_2 is apparently not the only factor involved in mediating growth differences between the sexes. We conclude this because (1) sexually related dimorphic growth resulted from both greater food consumption and higher FCE in females than males and (2) E_2 had no effect on the FCE of perch fed to satiation. One explanation for the higher FCE in females is that androgens may partially mediate sexually related dimorphic growth by suppressing FCE and growth in male perch. In support of this hypothesis, we have shown that exogenous androgens can retard perch growth (Malison et al. 1985). Additionally, increasing serum levels of androgens (Malison 1985) and the onset of spermatogenesis (Malison et al. 1986) in male perch occur coincidentally with the onset of sexually related dimorphic growth.

The results of experiment 2 (Table 4) indicate that intraspecific competition between the sexes is not a factor in sexually related dimorphic growth in perch. Brown (1957) and Brett (1979) have noted that among some fishes, intraspecific social

hierarchies develop in which "dominant" fish grow faster than "subordinate" fish, especially when food supply is limited. We found no evidence that if such hierarchies exist in perch, they are related to sex.

The mechanism(s) by which E_2 stimulates food consumption and growth in perch remains unknown. Estrogens are not generally considered to have direct anabolic effects on muscle or bone (Daughaday 1981). Exogenous estrogens theoretically could promote perch growth indirectly, by affecting the release or action of other (potentially anabolic) hormones. Estrogens stimulate the release of pituitary growth hormone (GH) in some mammals (Preston 1975; Daughaday 1981) and may have a similar effect in some species of fish (Olivereau and Olivereau 1979; Olivereau et al. 1986). However, GH-mediated growth stimulation in fishes (as well as mammals) has generally been associated with increases in FCE and changes in carcass composition (see Heitzman 1974, 1978; Donaldson et al. 1979; Daughaday 1981 for reviews). These effects were specifically not observed in E_2-treated perch. Estrogens have been shown to enhance pituitary release of prolactin in some fishes (Olivereau and Olivereau 1979; Barry and Grau 1986), but to our knowledge a definitive role for prolactin in controlling food consumption and growth in teleosts has not been demonstrated. The likelihood that E_2 promotes perch growth by increasing circulating thyroid hormone levels is low. Several investigators have reported that estrogens *reduce* circulating thyroid hormone levels in fish (Olivereau et al. 1981; MacLatchy et al. 1986; Cyr et al. 1988). Furthermore, our own studies (Malison et al. 1985) have demonstrated that exogenous thyroid hormones do not promote growth in perch as they do in several other fishes (most notably salmonid species; see Donaldson et al. 1979).

Another possible mechanism is that E_2 acts on neural appetite control centers in perch. In fish, these centers are probably located in the hypothalamus, just as in other vertebrates (Peter 1979). In some mammals, like the rat, estrogens can influence food consumption by acting on such centers (Bray 1974; Fishman 1976). Regardless of mechanism, our results show that E_2 stimulation of food consumption plays an important, but not exclusive, role in mediating sexually related dimorphic growth of perch. Our observations that female perch have higher FCEs than males (experiment 1) and that androgens can suppress perch growth (Malison et al. 1985) clearly suggest that sexually related dimorphic growth in this species is a complex process that probably involves several hormones.

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Fish Assemblage Stability in a Southern Appalachian Stream

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We monitored fish populations at three sites in a southern Appalachian stream system during a 40-mo study. Assemblages at two sites, consisting of four and five resident species, were persistent in terms of relative species abundances and production. This persistence was related to low variation in abundance of the two numerically dominant fishes, mottled sculpins (*Cottus bairdi*) and longnose dace (*Rhinichthys cataractae*). Less abundant residents, rosyside dace (*Clinostomus funduloides*), rainbow trout (*Salmo gairdneri*), and greenside darters (*Etheostoma blennioides*), displayed lower levels of persistence. We also observed pronounced annual variation in either young-of-the-year recruitment and/or subsequent year-class strength of four resident species, possibly resulting from a severe drought during the third year of study. Abundance and production of rosyside dace and trout were greatly affected by fluctuations in recruitment and year-class strength, suggesting that environmental variability strongly influenced these populations. Density-dependent mechanisms may have regulated sculpin and longnose dace populations. The three-species asssemblage at a third site also was persistent as a result of relatively stable sculpin and longnose dace populations, whereas the rainbow trout population fluctuated among years. We observed significant intersite differences in relative year-class strength in a given year and in population structures of sculpins and longnose dace, suggesting that spatial variation in habitat characteristics affected assemblage dynamics and responses to environmental fluctuations.

Une étude de 40 mo consistait à surveiller des populations de poissons à trois emplacements différents d'un cours d'eau situé dans le sud des Appalaches. Les groupements de poissons dans deux emplacements, constitués de quatre ou cinq espèces indigènes, étaient persistants en ce qui concerne l'abondance relative des espèces et la production. On a relié cette persistance à la faible variation d'abondance des deux espèces de poissons dominantes par leur nombre, soit les chabots tachetés (*Cottus bairdi*) et les naseux des rapides (*Rhinichtys cataractae*). Les espèces indigènes moins abondantes comme le méné long (*Clinostomus funduloides*), la truite arc-en-ciel (*Salmo gairdneri*) et le dard vert (*Etheostoma blennioides*), ont présenté des persistances moins élevées. Nous avons également observé une variation annuelle prononcée dans le recrutement des jeunes poissons de l'année et/ou dans l'effectif de la classe annuelle subséquente de quatre espèces indigènes, variation qui résultait probablement de la grave sécheresse ayant sévi au cours de la troisième année de l'étude. L'abondance et la production des ménés longs et des truites ont été très touchées par les fluctuations du recrutement et de la résistance de la classe d'âge; ceci laisse supposer que les variations de l'environnement influent fortement sur ces populations. Des mécanismes dépendant de la densité peuvent avoir assuré une régulation des populations de chabots et de naseux des rapides. Le groupement des trois espèces au troisième emplacement s'est également révélé persistant en raison de la stabilité relative des populations de chabots et de naseux des rapides, tandis que l'on a constaté des fluctuations de la population des truites arc-en-ciel au cours des années. Nous avons observé des différences significatives entre les emplacements, en ce qui concerne l'effectif relatif de la classe annuelle au cours d'une année donnée et les structures des populations de chabots et de naseux des rapides. Ce résultat porte à croire que la variation spatiale des caractéristiques de l'habitat a agi sur la dynamique des groupements et sur les réactions aux fluctuations de l'environnement.

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Interactive segregation frequently is implicated as the primary mechanism regulating the structure of stream fish assemblages (e.g. Zaret and Rand 1971; Gorman and Karr 1978; Moyle and Vondracek 1985), although unpredictable environmental disturbances (e.g. floods and droughts) also may substantially affect stream fish populations (Matthews 1986; and see citations in Grossman et al. 1982). Even though both mechanisms may organize stream fish assemblage structure, there is considerable disagreement over their relative importance (Herbold 1984; Yant et al. 1984; Grossman et al. 1985). Nonetheless, the influence of species interactions on assemblage organization depends on assemblage stability (Connell 1978; Sousa 1979; Grossman 1982; Grossman et al. 1982; Connell and Sousa 1983; but see Strong 1983). If assemblages are neither persistent or resilient (sensu Grossman 1982), it is unlikely that interactive segregation is the dominant factor regulating species abundances.

Long-term tests of persistence or resilience in stream fish assemblages have been uncommon. Studies of stream salmonids have documented extreme variation in abundance, often in response to flooding and subsequent habitat alteration (Seegrist and Gard 1972; Gard and Flittner 1974; Hall and Knight 1981; Waters 1983). Nonsalmonid fishes inhabiting two small California streams also displayed high year-to-year variation in

abundance, although assemblages generally were persistent in terms of species presence or absence (Sagehen Creek: Gard and Flittner 1974; Erman 1986; Martis Creek: Moyle and Vondracek 1985). Similarly, relative abundances of three to seven fishes in a desert stream were significantly correlated over 14 yr, although population sizes apparently fluctuated substantially (Aravaipa Creek: Meffe and Minckley 1987). Grosman et al. (1982) and Ross et al. (1985) examined variability in more diverse assemblages dominated by minnow species (Cyprinidae). Grossman et al. (1982) found nonsignificant among-year correlations of the relative abundances of the 10 most abundant fishes in Otter Creek, Indiana, over a 12-yr period. Ross et al. (1985) examined concordance between two population estimates made 9 yr apart in an Ozark stream (Piney Creek) and among four estimates made over 12 yr in Brier Creek, Oklahoma; species relative abundances were not significantly correlated in three of five stations in each stream. Pooled abundances for all Piney Creek stations, however, were significantly correlated (Ross et al. 1985), even when the analysis was extended to include samples taken after a major flood (Matthews 1986).

The importance of species interactions to assemblage organization may vary among streams possessing different faunas, geomorphologies, and disturbance regimes. An understanding of how regional characteristics contribute to differences in regulating mechanisms will require estimates of assemblage stability. Clearly, however, general conclusions regarding stability of lotic fish assemblages are not possible from the data currently available. This is due in part to the different techniques and criteria used by different investigators. For example, although measuring concordance among annual censuses may detect obvious instability (e.g. Grossman et al. 1982), significant concordance only implies a non-zero correlation among species abundances and does not necessarily demonstrate stability. Assemblages of widely fluctuating populations may appear concordant (e.g. Moyle and Vondracek 1985), and significant correlations are more likely as more species are included in analyses, or if a minority of species are consistently rare or abundant (Grossman et al. 1982, 1985; Rahel et al. 1984). Furthermore, frequent censusing during long-term studies, in conjunction with measurements of environmental fluctuations, may be necessary to infer mechanisms controlling species abundances. We have used this approach to study fish assemblage stability in a southern Appalachian drainage over a period of 40 mo. Specifically, we address the following: (1) is assemblage structure persistent (sensu Grossman 1982), both in terms of relative and absolute species abundances and production, and (2) is population variability related to fluctuations in stream flow? We also examine spatial variability in population and assemblage dynamics among three study sites.

Methods

Study Area

We monitored fish assemblages in Coweeta Creek and Ball Creek at the U.S. Forest Service Coweeta Hydrologic Laboratory (Macon County, North Carolina), located in the Blue Ridge Province of the southern Appalachian mountains. Mixed-hardwood forest predominates in the Coweeta basin, and rhododendron (*Rhododendron maximum* L.), mountain laurel (*Kalmia latifolia* L.), and dogwood (*Cornus florida* L.) line the stream margins. Coweeta streams generally have low ionic concentrations (Swank and Douglass 1975); alkalinity is <10 mg $CaCO_3 \cdot L^{-1}$ and conductivity normally is <20 $\mu mhos \cdot cm^{-1}$ at our study sites. The Coweeta basin has been protected from residential development and commercial timber harvesting since 1924; however, individual watersheds have been used for various experimental manipulations, including conversion to pasture, clear-cuting, and selective logging (Swank and Douglass 1975).

We selected three 30-m stream sections as permanent study sites. Hill and Grossman (1987) demonstrated that 30 m encompassed the home ranges of the three dominant fishes in Coweeta and Ball creeks. Thus, study sites were large enough for testing fish assemblage stability (Grossman 1982), yet were small enough to allow thorough sampling. Site 1 was located on fourth-order Coweeta Creek. Sites 2 and 3 were 460 and 730 m, respectively, upstream from Site 1 and were located on Ball Creek, a third-order tributary to Coweeta Creek. Sites 1 and 2 were physically and faunistically similar and were considered replicates. A concrete weir located 45 m upstream from Site 2 blocked upstream fish movement. Consequently, the fish assemblage in Site 3 was less diverse. Habitat at all sites included pools with depositional substrates, as well as runs and riffles with erosional substrates. Maximum stream depth normally was <1 m at all sites. Mean stream width was 6.2 m at Site 1 and 4.9 m at Sites 2 and 3, based on measurements made in autumn and winter 1982 and winter 1987. Stream widths fluctuated with discharge, however, which normally was highest from February through April and lowest from August through October.

Discharge and Temperature Measurements

Ball Creek discharge was monitored continuously at the weir between Sites 2 and 3. We used these recordings and long-term precipitation and discharge records for the Coweeta basin to compare stream flow during this study to 50-yr averages. We monitored stream temperature with continuously recording thermographs placed at Sites 1 and 3.

Population Estimation

We electrofished each study site every 2–3 mo from February 1984 to June 1987. We chose this time period because it met the temporal requirements for tests of assemblage stability proposed by Grossman (1982). Prior to sampling, block-nets were placed at upstream and downstream site boundaries. We then used a backpack electrofisher to generate a constant direct current electric field immediately upstream from a 0.25-in.-mesh seine held by two persons. Stunned fishes generally drifted into the seine and were immediately placed in water-filled styrofoam tanks. Beginning at the lower block-net and proceeding upstream, we typically made 3–4 equally timed electrofishing passes through the site. Captured fishes were measured (± 1 mm standard length (SL)) and weighed (± 1 g with spring scales, February 1984 – September 1985, or ± 0.1 g with an electric balance, November 1985 – June 1987). Fish mortality during sampling was rare, and fishes were returned to the stream after completion of the final electrofishing pass. Barrett and Grossman (1988) were unable to detect increased mortality associated with repeated electroshocking in Coweeta fishes; hence, sampling-related mortality probably did not strongly affect our results.

We used the computer program Capture (White et al. 1982) to estimate species' population sizes using the generalized

removal estimator. Capture also computed sampling variance and tested goodness of fit of the model to our data. Fishes present in low abundances were frequently captured only during the second or third pass through a site. In these cases we estimated population size as the total number of individuals caught, but could not estimate sampling variance or variance of annual production for these species (i.e. rainbow trout (*Salmo gairdneri*), rosyside dace (*Clinostomus funduloides*), and greenside darters (*Etheostoma blennioides*)). Also, on occasion the assumption of equal capture probability among passes was violated ($p<0.05$). We made population size estimates without confidence intervals for these cases and omitted these values from production estimates. Separate estimates were made for young-of-the-year (YOY) and adults for both sculpins and longnose dace; we distinguished these groups by differences in SL.

We estimated year-class strength as the number of age 1+ individuals present in the spring (mottled sculpins (*Cottus bairdi*) and longnose dace (*Rhinichthys cataractae*)) or autumn (rosyside dace) and assessed year-classes as weak, average, or strong in comparison with other year-classes at a particular site. We also estimated timing of YOY recruitment at each site as including all months in which we observed either smaller-sized or more YOY than in the previous collection.

Assemblage stability was assessed on the basis of (1) constancy in species relative abundances and (2) year-to-year population fluctuations of resident fishes. To quantify among year population variability, we separately calculated the coefficient of variation (c.v., expressed as a percentage) of species average abundances in spring (April–June 1984–87) and autumn (September–November 1984–86). We used spring and autumn estimates for among-year comparisons becaue we usually made two collections during each of these seasons, whereas we sampled less frequently in summer and winter. We also calculated c.v.'s using all collections; hence, these c.v.'s included variability resulting from both seasonal and annual population fluctuations. We used the following arbitrary criteria to classify populations based on their c.v.'s: (1) c.v. $\leq$ 25% = stable; (2) 26% $\leq$ c.v. $\leq$ 50% = moderately stable; (3) 51% $\leq$ c.v. $\leq$ 75% = moderately fluctuating; (4) c.v. $\geq$ 76% = fluctuating.

Annual Production

We used the size–frequency method (SFM) to estimate annual production, using procedures outlined by Krueger and Martin (1980) and Garman and Waters (1983). This method involves estimating the average number of individuals that grow through successive size-classes in a year and does not require a knowledge of individual ages. The method assumes, however, that individuals spend equal time in each size-class. Consequently, we used length-classes that were roughly equivalent to year-classes in our spring or summer samples. The SFM also requires an estimate of the average maximum lifespan (i.e. cohort production interval, or CPI (Benke 1979)). Based on length–frequency histograms, we assumed CPI values of 5 yr for mottled sculpins and 4 yr for longnose dace, rosyside dace, and greenside darters. These values generally agree with published estimates of average maximum lifespan for these species (Lachner et al. 1950; Davis 1972; Reed and Moulton 1973; Wolfe et al. 1978). We used a CPI of 2 yr for rainbow trout because we rarely observed older individuals in our sites.

The mean number of individuals present in each length-class on a given date was estimated from observed length-class proportions of our catch and the total population estimate provided by the program Capture. Variances in standing stocks of mottled sculpins and longnose dace for each length-class were computed from estimates of sampling variance and length-class proportion variance for that date (Newman and Martin 1983). From these values, we computed the average number and wet weight of fish in each length-class (and associated sampling variances) for each year (Krueger and Martin 1980; Garman and Waters 1983). We calculated production estimates by the formula given by Krueger and Martin (1980), using arithmetic mean weights (Garman and Waters 1983). All negative values (resulting from increased average standing stock between succesive length-classes) were included in production calculations, except those caused by low densities in the smallest length-class. We excluded the latter negative values because they could have resulted from low capture probabilities for very small fish. We calculated variances of production estimates by the method of Garman and Waters (1983), which incorporates measurement error of fish weight into the variance estimation method proposed by Krueger and Martin (1980).

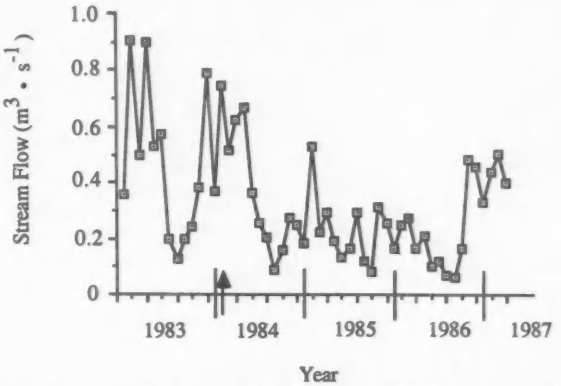

FIG. 1. Average maximum discharge in Ball Creek plotted for each month, January 1983 through April 1987. Vertical lines indicate January in each year; an arrow indicates our initial sampling date. Discharge was recorded at the weir between Sites 2 and 3.

Production was expressed as grams wet weight produced per year in each study site. Therefore, estimates were for populations in constant lengths of stream and were independent of variation in fish density caused by changes in stream width. We could not accurately calculate production per unit area because we did not measure temporal changes in stream area at the study sites.

Results

Flow and Temperature Variation

There were two periods of exceptional stream flow during our study. In May 1984, floods elevated monthly stream flow to approximately 1.9 times the 50-yr May average (Fig. 1). Flows in Coweeta Creek increased fivefold, and events of this magnitude occur approximately every 1–2 yr at Coweeta (J. Waide, Coweeta Hydrologic Laboratory, pers. comm.). The southeastern United States experienced a severe drought in 1985 and 1986; stream discharge from April to September 1986 was the lowest in the 50-yr record at the Coweeta Hydrologic Laboratory. The drought also eliminated normal winter high flows in early 1986; monthly stream flows were <50% of the

TABLE 1. Assemblage structure at the study sites. Fishes are listed as residents (R), seasonals (S), occasionals (O), or not present (–).

Species	Site 1	Site 2	Site 3
Mottled sculpin (*Cottus bairdi*)	R	R	R
Longnose dace (*Rhinichthys cataractae*)	R	R	R
Rainbow trout (*Salmo gairdneri*)	R	R	R
Rosyside dace (*Clinostomus funduloides*)	R	R	–
Greenside darter (*Etheostoma blennioides*)	R	O	–
Largescale stoneroller (*Campostoma oligolepis*)	S	S	–
Rockbass (*Ambloplites rupestris*)	S	S	–
Northern hogsucker (*Hypentelium nigricans*)	O	O	–
Fatlips minnow (*Phenacobius crassilabrum*)	O	–	–
Creek chub (*Semotilus atromaculatus*)	O	–	–
Warpaint shiner (*Notropis coccogenis*)	–	O	–
River chub (*Nocomis micropogon*)	–	O	–
Brook trout (*Salvelinus fontinalis*)	–	–	O

TABLE 2. Fish population size estimates (and 95% confidence intervals) for Site 1.

	1984					1985					1986						1987		
Species	Feb.	May	June	Sept.	Nov.	Feb.	April	June	Sept.	Nov.	Jan.	Mar.	May	July	Sept.	Nov.	Jan.	March	May
Mottled sculpin																			
Adults	61 (48–81)	40 (37–47)	35[a]	65 (57–77)	37[a]	58 (32–124)	48[a]	51 (44–64)	46 (38–61)	39 (21–96)	28 (26–34)	24 (24–36)	42 (36–53)	28 (26–34)	43 (43–46)	26 (23–34)	26 (25–30)	22 (19–30)	31[a]
Young-of-year	2[c]	12 (11–18)	0	2[b]	3 (3–4)	8 (7–14)	8 (7–14)	1	0	2[b]	2 (2–3)	1[b]	0	1[b]	7[b]	5 (5–6)	5 (5–7)	8 (7–14)	0
Longnose dace																			
Adults	18 (10–55)	7 (7–10)	48 (39–64)	16 (16–18)	12 (12–14)	4 (4–5)	17 (17–20)	20 (19–24)	8 (8–10)	6[b]	4 (4–6)	2[b]	35 (25–59)	10 (10–12)	7 (7–8)	6[b]	6[b]	8 (8–10)	10[a]
Young-of-year	3[c]	2[b]	0	0	1[b]	1[b]	2[b]	0	0	1	0 (1–2)	0	0	0	0	0	1[b]	0	0
Rosyside dace	0	3[b]	1[b]	7 (7–10)	9 (9–10)	0	8 (7–14)	6 (6–10)	5 (5–6)	2 (2–3)	0	0	9 (9–11)	8 (8–12)	23 (23–26)	3 (3–4)	2[b]	0	8[a]
Rainbow trout, all	2[c]	1[b]	7 (7–10)	3 (3–4)	2[b]	3 (3–5)	3[b]	9 (9–11)	9 (9–10)	4 (4–6)	1[b]	2 (2–3)	8[b]	4 (4–5)	4 (4–6)	4 (4–6)	4[a]	4[b]	0
Young-of-year[d]	0	0	7	3	2	0	2	7	9	4	0	0	3	3	4	3	0	0	0
Greenside darter	8 (6–18)	2[b]	2[b]	2[b]	6 (6–8)	3 (3–4)	4 (2–6)	4 (4–5)	2[b]	3 (3–5)	2[b]	1[b]	3 (3–5)	2[b]	1[b]	1[b]	2[b]	0	0
Stoneroller	2[c]	1[b]	0	0	14 (14–15)	15 (14–20)	6 (2–10)	1 (1–2)	0	5 (5–8)	2 (2–3)	3[b]	3[b]	0	0	3 (3–4)	7[a]	4 (4–5)	1 (1–2)
Rockbass	0	0	0	0	1 (1–2)	2[b]	0	0	1[b]	1[b]	0	1[b]	0	0	0	1[b]	3[b]	1 (1–2)	0

[a]Assumption of equal probability of capture is violated ($p < 0.05$); hence, a confidence interval was not estimated.
[b]There was no depletion between passes; value shown is the total number of individuals captured and is a minimum estimate of population size.
[c]All individuals were captured on the first of two passes; consequently a confidence interval cannot be calculated.
[d]Rainbow trout YOY also are included in the population estimates for all rainbow trout.

average values for January–March. Mean and maximum water temperatures during summer 1986 were 17 and 19°C (Site 1) and 16.5 and 18°C (Site 3), approximately 1° higher than in the previous two summers.

Assemblage Structure and Persistence

Sites 1 and 2

Assemblages at Sites 1 and 2 consisted of resident, seasonal, and occasional species (Table 1). Residents were present during all samples, whereas the two seasonals were abundant only in autumn and winter (rockbass) or autumn through early spring (largescale stonerollers (*Campostoma oligolepis*); Tables 2 and 3). Occasional species either were collected only once or twice or did not display a seasonal pattern of occcurrence. We could not assess variability in populations of seasonal or occasional species. Our resident assemblages, therefore, were subsets of larger fish assemblages; however, the majority of individuals belonged to resident species. For example, of the occasionals, only northern hogsuckers (*Hypentelium nigricans*) were represented by more than two individuals in a collection.

Relative abundances of residents were constant at Sites 1 and 2 during the 3 yr of study (Tables 2 and 3). Mottled sculpins numerically dominated assemblages at both sites followed by

TABLE 3. Fish population size estimates (and 95% confidence intervals) for Site 2.

	1984					1985					1986						1987		
Species	Feb.	May	June	Sept.	Nov.	Feb.	May	June	Sept.	Nov.	Jan.	Mar.	May	July	Sept.	Nov.	Feb.	April	May
Mottled sculpin																			
Adults	76 (69–86)	52 (45–64)	44 (40–52)	60 (46–83)	86 (40–204)	29 (29–32)	43 (39–51)	43 (37–55)	61[a]	76 (50–120)	31 (30–36)	31 (23–51)	62 (56–72)	51 (50–55)	48 (44–56)	60 (50–76)	82 (54–128)	31 (30–35)	71 (69–75)
Young-of-year	3[b]	0	1[b]	10[b]	7 (7–8)	4[b]	0	0	47 (43–55)	53[b]	40 (31–59)	42 (33–60)	0	4[b]	23 (22–28)	10[b]	39 (33–51)	62[b]	0
Longnose dace																			
Adults	14[b]	16 (13–26)	21[a]	25 (23–32)	32 (22–57)	23 (18–38)	17 (16–21)	13 (13–16)	11 (10–15)	11 (11–13)	7 (7–8)	12 (11–18)	15 (15–16)	13 (12–18)	8 (8–9)	18 (15–27)	11 (10–15)	11[b]	23 (22–27)
Young-of-year	7[b]	2[b]	0	1[b]	2[b]	5[b]	3[b]	0	5[a]	14 (10–30)	4 (4–6)	7[b]	4 (4–6)	0	3 (3–4)	5 (5–6)	10 (10–11)	5 (5–6)	0
Rosyside dace	0	1[c]	4[a]	9 (9–10)	16 (16–19)	0	1 (1–2)	13 (13–14)	5 (5–7)	6[b]	3 (3–4)	1[b]	7 (7–10)	8 (8–11)	18 (18–20)	10 (10–12)	1 (1–2)	0	3 (3–5)
Rainbow trout, all	1[c]	1[c]	7 (7–9)	4 (4–6)	2[b]	3 (3–4)	2 (2–3)	8 (8–11)	8 (8–10)	3[b]	3 (3–4)	6 (6–8)	17 (14–29)	8[a]	11 (11–13)	6 (6–10)	3 (3–5)	2[b]	1 (1–2)
Young-of-year[d]	0	0	6	4	1	0	0	7	6	1	0	0	17	7	10	5	0	0	0
Stoneroller	1[b]	2[c]	1 (1–2)	1 (1–2)	31 (31–33)	16 (15–22)	1 (1–2)	0	0	6 (6–7)	13 (13–15)	5 (5–7)	0	0	0	13 (12–18)	8 (8–9)	8 (8–9)	2[a]
Rockbass	0	0	0	0	0	0	0	0	0	2 (2–3)	2[b]	0	0	0	0	1[b]	0	0	0

[a]Assumption of equal probability of capture is violated ($p < 0.05$); hence, a confidence interval was not estimated.
[b]There was no depletion between passes; value shown is the total number of individuals captured and is a minimum estimate of population size.
[c]All individuals were captured in the first of two passes; consequently a confidence interval cannot be calculated.
[d]Rainbow trout YOY also are included in the population estimates for all rainbow trout.

TABLE 4. Coefficients of variation (%) of species abundances computed for spring (S), autumn (A), and all (All) samples for residents at each site.

	Site 1			Site 2			Site 3		
Species	S	A	All	S	A	All	S	A	All
Sculpins	23	15	31	30	28	36	14	33	44
Longnose dace	49	46	86	9	30	30	22	27	37
Rainbow trout	76	47	67	101	49	82	85	74	77
Rosyside dace	48	58	112	51	43	99	—	—	—
Greenside darters	76	60	77	—	—	—	—	—	—

TABLE 5. Fish population size estimates (and 95% confidence intervals) for Site 3.

	1984				1985					1986					1987	
Species	Feb.	June	Sept.	Nov.	Feb.	May	July	Sept.	Nov.	Jan.	April	May	July	Dec.	April	June
Mottled sculpin																
Adults	115 (62–211)	43 (37–55)	55 (50–63)	47 (40–60)	61 (33–131)	37 (31–50)	37 (26–64)	37 (27–59)	42 (36–53)	29 (27–35)	40 (27–70)	27 (21–42)	33 (30–41)	33 (32–37)	48 (39–64)	38 (33–48)
Young-of-year	0	1 (1–2)	9 (7–22)	22 (15–46)	7[b]	3[b]	0	5 (5–6)	6[b]	2[b]	1[b]	0	0	2[b]	8 (8–10)	0
Longnose dace																
Adults	16 (15–22)	16 (15–20)	31 (29–38)	18 (18–20)	33 (22–27)	20 (18–27)	15 (15–18)	33 (21–67)	16 (16–19)	14[a]	14 (14–15)	16 (16–18)	23 (17–42)	16 (14–23)	12 (12–14)	11 (10–15)
Young-of-year	3 (3–5)	0	4 (4–7)	2[b]	0	0	0	2 (2–3)	1[b]	0	2[b]	0	0	0	1 (1–2)	0
Rainbow trout, all	1[b]	7 (7–9)	6 (6–9)	2 (2–3)	3 (3–4)	1[b]	6 (6–8)	1[b]	2 (2–3)	1[b]	3[b]	2 (2–3)	4 (4–5)	1 (1–2)	0	4 (4–6)
Young-of-year[c]	0	6	6	2	0	0	6	1	2	0	0	1	3	1	0	1

[a]Assumption of equal probability of capture is violated ($p < 0.05$); hence, a confidence interval was not estimated.
[b]There was no depletion between passes; value shown is the total number of individuals captured and is a minimum estimate of population size.
[c]Rainbow trout YOY also are included in the population estimates for all rainbow trout.

longnose dace. Rosyside dace and rainbow trout displayed similar levels of abundance (rarely more than 10 in these 30-m sections), and we usually found fewer than five darters (Site 1).

Although relative abundances generally were stable, absolute abundances fluctuated both seasonally and annually at Sites 1 and 2 (Tables 2 and 3). Adult sculpin abundance decreased from 1984 through 1987 at Site 1 (Table 2), whereas YOY increased in 1985 and 1986 at Site 2 (Table 3). Sculpin populations appeared moderately stable at both sites; spring and autumn c.v.'s were 30% or less and c.v.'s based on all collections (which incorporated seasonal variation) were 31 and 36% at Sites 1 and 2, respectively (Table 4). Longnose dace also appeared stable at Site 2, whereas the Site 1 population fluctuated among years (Table 4). Adult longnose dace were more abundant in autumn 1984 than in autumn of both 1985 and 1986 at both Sites 1 and 2 (Tables 2 and 3). The YOY recruitment, however, was higher at Site 2 in 1985 and 1986, thereby increasing population estimates and reducing among-year variation (the autumn c.v. for adults was 55% at Site 2). Greater fluctuations in longnose dace abundance at Site 1 also resulted from spring increases in adults, possibly in association with spawning (Table 2).

Rosyside dace fluctuated in numbers at both Sites 1 and 2. Populations usually increased in autumn (Tables 2 and 3) when we first collected age 1+ individuals (we were unable to sample age 0+ rosyside dace effectively). Abundances then declined during winter, either because dace overwintered outside of our sites or because they were in refuges (e.g. under stones, J. Hill, pers. obs.) and thus less vulnerable to electrofishing. These seasonal fluctuations produced c.v.'s of 99 and 112% computed across all samples (Table 4). In addition, seasonal abundances of rosyside dace fluctuated among years, with spring and autumn c.v.'s ranging from 43 to 58% (Table 4).

Rainbow trout populations also displayed high variability at Sites 1 and 2, especially among spring samples (Table 4). Trout abundance peaked in late spring or early summer, when we initially captured YOY, and declined through autumn and winter (Tables 2 and 3). Age 0+ and 1+ trout predominated at our study sites; we observed few individuals older than 18 mo. Consequently, high spring c.v.'s reflect among-year variation in YOY recruitment. For example, at Site 1 we observed fewer YOY in 1986 in comparison with previous years, whereas YOY recruitment in 1986 was high at Site 2 (Tables 2 and 3).

Greenside darters displayed irregular fluctuations in abundance at Site 1 (Tables 2 and 4) and were present only occasionally in Site 2. Apparent population increases in February and November 1984 resulted from immigration of adults (approximately 2 yr old). Juvenile darters (age 0+ to 1+) either were not present or were not sampled at our sites. Darters were absent in spring 1987. In addition, variable numbers of stonerollers immigrated during autumn and winter (Tables 2 and 3); c.v.'s for November–March (1984–87) were 81 and 59% at Sites 1 and 2, respectively. Abundances of rockbass (*Ambloplites rupestris*) from autumn to winter varied from 0 to 3.

Site 3

Sculpins, longnose dace, and rainbow trout, in decreasing order of abundance, were the resident species at our most upstream site (Site 3; Tables 1 and 5). Sculpin and longnose dace populations appeared moderately stable, with seasonal c.v.'s of 33% or less (Table 4). Rainbow trout abundances fluctuated considerably, including low YOY recruitment in 1986 (Tables 4 and 5).

Year-Class Strength and the Recruitment Period

We observed pronounced among-year variation in year-class strength (number of YOY surviving to age 1+) for sculpins, longnose dace, and rosyside dace (Table 6). The 1985 and 1986 sculpin year-classes were especially abundant (i.e. during spring 1986 and 1987) at Site 2, although these year-classes were average or weak at Site 1. Similarly, the 1986 longnose dace year-class was strong only at Site 2, whereas the 1985 year-class was weak at Site 1. Rosyside dace had weak 1984 year-classes followed by strong 1985 year-classes at both Sites 1 and 2 (Table 6). Thus, the drought years produced strong year-classes of sculpins, longnose dace, and rosyside dace, as well as high abundances of YOY trout, in Site 2. At Site 1, however, only rosyside dace produced a strong year-class during the drought. At Site 3 we observed fewer YOY trout in 1986 and the drought had no apparent effect on sculpin or longnose dace year-classes (Table 6).

Periods of YOY recruitment also varied among years and sites (Table 7). Sculpin YOY generally became abundant in autumn but recruitment often persisted into winter at Site 1. We observed high winter recruitment at Sites 2 and 3 only in 1986–87. Longnose dace recruitment also occurred later at Site 1 and in 1986–87. We generally observed earlier recruitment of trout at Site 1, although early trout recruitment occurred in all sites during spring 1986.

Production

Sculpins and trout generally dominated production in these assemblages (Table 8). Sculpin production was high because the species was abundant, whereas trout grew faster (in absolute units) and attained a larger average size than other residents. Longnose dace production was significantly ($p<0.05$) lower than that of sculpins in two of three years at each site. Rosyside dace and darters had the lowest production values; however, these values probably underestimated actual production because age 0+ individuals were not included. Similarly, we probably

TABLE 6. Year-class estimates: 95% confidence intervals for the number of individuals born in a given year which survived to age 1. Relative year-class strength is shown in parentheses (W = weak, A = average, S = strong).

	Sculpins			Longnose dace			Rosyside dace	
Year	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2
1983	12–19(A)	3–7(W)	13–48(A)	2–6(A)	7–14(A)	1–3(A)	6–9(A)	15–18(S)
1984	10–20(A)	9–16(A)	14–36(A)	3–7(A)	6–10(A)	0 (W)	1–3(W)	0 (W)
1985	6–13(W/A)	37–51(S)	3–8(W)	0 (W)	9–14(A)	2–4(A)	8–14(S)	8–13(S)
1986	10–24(A)	48–57(S)	11–20(A)	3–6(A)	14–20(S)	1–3(A)	—	—

TABLE 7. Young-of-year recruitment periods for 1984–86 by species and site.

Species	Year	Site 1	Site 2	Site 3
Sculpins	1984	Sept.–Feb.	June–Sept.	June–Nov.
	1985	June–Jan.	Sept.–Nov.	Sept.–Nov.
	1986	July–Sept.	July–Apr.	Dec.–Apr.
Longnose dace	1984	Nov.–Apr.	Sept.–Feb.	Sept.
	1985	Nov.	Sept.–Mar.	Sept.
	1986	Jan.–May	Sept.–Feb.	Apr.
Rainbow trout	1984	June	June	June
	1985	Apr.–Sept.	June	July
	1986	May–July	May	May–July

TABLE 8. Annual production (grams wet weight per 30 linear m of stream) ± 2 SE for sculpin and longnose dace.

Year	Sculpins	Longnose dace	Rainbow trout	Rosyside dace[a]	Greenside darters	Total
Site 1						
1984	154 ± 33	52 ± 12	80	10	15	311
1985	113 ± 33	30 ± 7	123	12	12	290
1986	82 ± 12	62 ± 31	109	30	6	289
Site 2						
1984	124 ± 23	75 ± 31	112	16	—	327
1985	103 ± 13	40 ± 14	96	18	—	257
1986	104 ± 12	33 ± 8	196	25	—	358
Site 3						
1984	155 ± 33	64 ± 13	155[b]	—	—	374
1985	114 ± 24	71 ± 17	15	—	—	200
1986	85 ± 17	64 ± 26	58	—	—	207

[a]Rosyside dace estimates are for the months of May–November.
[b]Production = 33 g if a single age 2+ individual (weight = 66 g) is excluded from calculations.

TABLE 9. Average (±2 SE) number of sculpin and longnose dace in successive length-classes (mm SL).

	Sculpins					Longnose dace			
Year	≤35	36–50	51–60	61–70	>70	≤45	46–65	66–80	>80
Site 1									
1984	9 ± 5	24 ± 8	21 ± 8	7 ± 3	1 ± 1	3 ± 1	4 ± 2	8 ± 2	3 ± 1
1985	7 ± 5	20 ± 9	21 ± 9	4 ± 3	1 ± 1	1 ± 1	<1	6 ± 2	4 ± 2
1986	4 ± 2	14 ± 3	14 ± 3	2 ± 1	1 ± 1	0	2 ± 2	12 ± 8	3 ± 2
Site 2									
1984	8 ± 4	19 ± 5	23 ± 7	6 ± 3	1 ± 1	7 ± 4	17 ± 7	6 ± 3	0
1985	24 ± 5	20 ± 5	16 ± 4	5 ± 2	1 ± 1	9 ± 3	7 ± 3	4 ± 2	<1
1986	27 ± 5	27 ± 4	10 ± 3	5 ± 2	1 ± 1	6 ± 2	7 ± 2	1 ± 1	1 ± 1
Site 3									
1984	13 ± 6	18 ± 6	15 ± 8	14 ± 5	8 ± 4	4 ± 2	8 ± 2	9 ± 2	2 ± 1
1985	9 ± 4	18 ± 6	11 ± 5	6 ± 3	6 ± 4	1 ± 1	10 ± 3	8 ± 3	2 ± 2
1986	2 ± 1	19 ± 5	8 ± 4	4 ± 2	3 ± 2	2 ± 2	11 ± 6	5 ± 3	2 ± 1

underestimated YOY abundances for sculpins and longnose dace.

Our estimates indicated that annual fish production was <3 g wet wt.·m^{-2} at all sites. Estimates of total assemblage production generally were similar among sites (Table 8), even though Site 1 was approximately 26% wider than Sites 2 and 3. Hence, we saw no evidence that fish production or abundance per unit length of stream increased with increasing stream area. In addition, species-specific production estimates were similar at Sites 1 and 2 (Table 8). At Site 3, longnose dace

production was consistently higher than at Sites 1 and 2; these differences were significant ($p < 0.05$) in 1985. Trout production at Site 3, however, appeared consistently lower than at the downstream sites, especially if a single age 2+ individual was excluded from the 1984 Site 3 estimate (Table 8).

Production by water-column species (i.e. rosyside dace and trout) generally increased during the 1986 drought (Table 8). Higher production by rosyside dace (Sites 1 and 2) and trout (Site 2) during 1986 resulted from increased abundances of age 1+ and 0+ individuals, respectively. In contrast, production by benthic fishes did not increase despite strong year-classes at Site 2. Longnose dace production was lower in 1986 at Site 2, as was production during 1986 by sculpins at Sites 1 and 3 and by darters at Site 1.

Intersite Differences in Population Structure

Population structures of the numerical dominants appeared relatively stable, although even for these species, YOY abundances generally varied more than abundances of older (i.e. larger) individuals (Table 9). We did, however, observe consistent differences among sites in population structures. Based on average cohort data, large sculpins (≥70 mm SL) were common only at Site 3, whereas YOY usually were most abundant at Site 2 (Table 9). Longnose dace YOY similarly were abundant only at Site 2. Conversely, large dace (>65 mm SL) composed 61–88% of the average cohorts at Site 1, in contrast with 13–23% at Site 2 (Table 9). Most longnose dace in Site 3 were of intermediate length (46–80 mm SL).

Discussion

The assemblages of resident fishes in Coweeta and Ball creeks appeared persistent in terms of relative abundances of species during 40 mo. That is, sculpins and longnose dace always were more abundant than trout or rosyside dace and darters usually were rare. Assemblage persistence primarily resulted from low variation in sculpins and longnose dace. These species exhibited low among-year variation in abundance and production despite fluctuations in YOY recruitment and year-class strength. For example, year-classes were strong in one site following a drought, indicating that changes in stream flow significantly affected recruitment and/or YOY survival. Variation in reproductive success did not strongly affect total abundances, however, which suggested that density-dependent mechanisms, such as intra- and interspecific competition for food or space, primarily regulated sculpin and longnose dace populations.

Trout and rosyside dace populations were more variable, in part because new recruits (i.e. YOY trout and age 1+ dace) composed larger proportions of their populations. It also is possible that trout home ranges exceeded our 30-m study sites, thereby increasing variability among population estimates. Whitworth and Strange (1983), however, reported that most trout moved less than 30 m in a year in a similar southern Appalachian stream. Moreover, trout variation in our sites primarily resulted from annual variation in YOY recruitment. We do not believe that this variation was an artifact of sampling variability because YOY abundances generally were consistent among summer and autumn samples for a given year.

Standing stocks of age 1+ trout generally varied from zero to three, despite annual variation in YOY recruitment. Hence, either harsh environmental conditions or density-dependent mortality (or emigration) limited YOY survival or residency in our sites. Also, we rarely collected age 2+ or older individuals. High overwinter mortality and weight loss have been cited for age 2+ and 3+ rainbow trout in both fished and unfished southeastern Appalachian streams (Whitworth and Strange 1983; Neves et al. 1985; Durniak and England 1986). We did not measure fishing mortality, but assume that it was low because we rarely observed anglers during more than 5 yr of fieldwork.

Abundances of rosyside dace displayed relatively high year-to-year variation of both age 1+ and older individuals, suggesting that environmental variability had a stronger effect on populations than did density-dependent mechanisms. Few age 1+ rosyside dace were recruited in autumn 1985, possibly as a result of floods in spring 1984, whereas strong year-classes followed drought conditions of 1985. Although we did not directly sample YOY, our observations suggest that stream flow subsantially influenced YOY recruitment. Variation in annual discharge also may have influenced adult survival. Hill and Grossman (1987) observed downstream displacement of mature rosyside dace in Coweeta Creek following the spring 1984 floods. Moreover, individuals were displaced from a stream section with few apparent refuges to a section with more potential refuges; there was no evidence that sculpins or longnose dace, both benthic dwellers, were displaced by flooding (Hill and Grossman 1987).

In summary, our data sugest that density-dependent mechanisms primarily regulated Coweeta populations of sculpins and longnose dace, whereas unpredictable environmental fluctuations had a strong influence on abundances of rosyside dace and trout YOY, and possibly on trout survival. Changes in stream flow, however, apparently affected YOY recruitment and/or survival of all species in some habitats. Among-year variation in YOY recruitment could have resulted either from variable larval production or changes in larval drift into and out of our sites. Other researchers have correlated among-year variability in the timing, duration, and amplitude of water-level fluctuations with the reproductive success of stream fishes (Starrett 1951; Larimore 1954; Ross and Baker 1983; Waters 1983; Moyle and Vondracek 1985; Schlosser 1985; Erman 1986). Water temperature also may vary with stream flow regime and influence juvenile growth and year-class strength (Mills and Mann 1985). We observed only small increases in water temperature during the 1985–86 Coweeta drought and observed no apparent effects on growth. Temperature increases during 1986, however, may have extended YOY recruitment later into winter (sculpin and longnose dace) and/or allowed earlier recruitment of trout in the spring.

Variable recruitment and survival contributed to annual differences in production estimates. Fish production at Coweeta was low compared with more nutrient rich streams in the southeast (Lotrich 1973; Small 1975; Neves and Pardue 1983; Whitworth and Strange 1983; Neves et al. 1985), although Michaels (1978) observed similarly low production of brook trout in three north Georgia streams. Our estimates indicate, however, that increased YOY recruitment (such as we observed following the 1985–86 drought) could double annual production by trout and rosyside dace. The strong year-classes of sculpin and longnose dace at Site 2 could eventually increase production if these individuals were to survive to larger sizes (i.e. depending on the relative strength of density-dependent regulation in these populations).

Annual population changes were not parallel among our three study sites, illustrating the importance of spatial heterogeneity in assemblage dynamics and the potential interaction of habitat type and environmental variability. For example, the effect of the 1986 drought on trout recruitment varied among sites: we observed YOY increases in one site and decreases in two other sites. Persistent intersite differences in size distributions of sculpin and longnose dace also suggested site-specific differences in reproductive success and/or YOY recruitment. Erman (1986) and Moyle and Vondracek (1985) also observed intersite heterogeneity in size–frequencies of sculpins and speckled dace, respectively. These observations underscore the necessity of sampling stream fishes in multiple sites within a system; environmental effects and assemblage dynamics may vary among sites depending on local habitat and population structures. Ross et al. (1985) and Matthews (1986) similarly emphasized the importance of sampling multiple sites within a stream or watershed. These authors combined data from different sites to test stability of fish assemblages at a watershed level. Because coexistence of interacting populations is the property of interest in tests of assemblage stability, we suggest that sites should be analyzed separately unless it is known that populations interact among sites. For example, it would be inappropriate to pool data from our study sites because the dominant fishes have limited home ranges and individuals at different sites are unlikely to interact.

Moyle and Vondracek (1985) suggested that the fish assemblage of Martis Creek, a small coldwater California stream, is persistent, and that species (and age-classes) partition microhabitat and food resources. We similarly suggest that mottled sculpin and longnose dace populations in Coweeta are stable (= persistent); however, populations of rosyside dace and young trout are much less stable (= nonpersistent), probably in response to variable discharge patterns. Stream assemblages dominated by short-lived, rapidly maturing water-column fishes may generally show greater variability corresponding to environmental fluctuations, such as documented by Grossman et al. (1982) and Ross et al. (1985). In contrast with Moyle and Vondracek's (1985) observations, Grossman and Freeman (1987) saw no evidence of microhabitat partitioning among benthic or water-column fishes at Coweeta. Food availability may limit the more stable species, and we are investigating this possibility in our current research.

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Magnitude of Blue-Green Algal Blooms in a Saline Desert Lake Evaluated by Remote Sensing: Evidence for Nitrogen Control

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Galat, D. L., and J. P. Verdin. 1988. Magnitude of blue-green algal blooms in a saline desert lake evaluated by remote sensing: evidence for nitrogen control. Can. J. Fish. Aquat. Sci. 45: 1959–1967.

Seventy-six percent of the 1972–86 variability in remotely sensed maximum surface water biomass of *Nodularia spumigena* blooms in Pyramid Lake, Nevada, was explained by concentrations of surface water total nitrogen (TN) during the preceding winter circulation. Very large summer–autumn *Nodularia* blooms were recorded by Landsat subsequent to low early winter surface water TN concentrations, very low fluvial discharge, and fluvial TN loads as predicted, but contrary to predictions, also when fluvial discharge and TN loads were very high. The observed cause of large *Nodularia* blooms following high fluvial nitrogen influx was temporary meromixis produced by the large volume of freshwater transporting this nitrogen. Incomplete winter lake circulation reduced internal transport of hypolimnetic nitrogen to surface waters. Meromixis resulted in early stable summer thermal stratification and early depletion of epilimnetic inorganic nitrogen, followed by early and large *Nodularia* blooms. Variations in magnitude of historic *Nodularia* blooms in a saline desert lake support the generality of blue-green algal dominance in lakes with low nitrogen and high phosphorus concentrations (i.e. low N:P ratios). However, climatic forcing of fluvial discharge and lake mixing patterns were also shown to be important determinants of seasonal succession of phytoplankton to blue-greens.

La variabilité observée par télédétection, entre 1972 et 1986, de la biomasse maximale en eau superficielle des proliférations de *Nodularia spumigena* dans le lac Pyramid, Nevada, a été expliquée à 76 % par la concentration en azote total dans la tranche superficielle d'eau lors de la période précédente de circulation d'eau de l'hiver. De très importantes proliférations estivales et d'automne de *Nodularia* ont été enregistrées par Landsat à la suite de périodes de faible concentration en azote total au début de l'hiver dans la tranche d'eau superficielle, d'un très faible écoulement fluvial et d'une charge fluviale en azote total conforme aux prévisions, mais, contrairement à ces dernières, aussi lorsque l'écoulement fluvial et la charge en azote total étaient très élevés. L'état méromictique temporaire du lac, attribuable au volume élevé d'eau douce qui transportait cet azote, a été considéré comme la cause observée des importantes proliférations de *Nodularia* après un grand apport d'azote d'origine fluviatile. La circulation incomplète de l'eau dans le lac durant l'hiver a réduit le transport interne d'azote provenant de l'hypolimnion vers la surface. Tôt en été, l'état méromictique a créé une stratification thermique stable et conduit à un épuisement hâtif de l'azote inorganique dans l'épilimnion, qui a été suivi par des proliférations hâtives et étendues de *Nodularia*. Les variations d'étendue des proliférations passées de *Nodularia* dans un lac salé de désert vont dans le sens d'une dominance des algues bleues dans les lacs pauvres en azote et riches en phosphore (c.-à-d. de faibles rapports N:P). Cependant, il est montré que le forçage climatique de l'écoulement fluvial et le brassage de l'eau dans le lac constituent également d'importants déterminants de la succession saisonnière phytoplancton – algues bleues.

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Dominance of blue-green algae in lakes and estuaries has long been associated with low nitrogen to phosphorus (N:P) ratios (Forsberg et al. 1978; Niemi 1979; Smith 1982). According to resource competition theory, the ability of many cyanophytes to fix atmospheric nitrogen gives them a competitive advantage over diatoms and green algae when nitrogen is limiting but phosphorus is abundant, i.e. N:P ratios are low (Tilman et al. 1982, 1986). Recent correlative analyses encompassing a large number of lakes (Smith 1983a, 1986) and within a single lake over 5 yr (McQueen and Lean 1987) corroborate this theory. Contrary evidence exists, however (Trimbee and Prepas 1987), and significance of correlations vary depending on which fractions of nitrogen and phosphorus are considered (McQueen and Lean 1987). Furthermore, other environmental variables are also important predictors of nitrogen-fixing blue-green algal biomass, such as water temperature (Tilman et al. 1986; McQueen and Lean 1987), water column stability (Reynolds 1984), and light (Smith 1986).

Support for Tilman et al.'s (1982, 1986) proposition comes from many studies where experimental additions of nitrogen to lakes or enclosures in lakes resulted in reduced dominance by nitrogen-fixing cyanophytes (Schindler 1977; Lean et al. 1978; Barica et al. 1980; Flett et al. 1980; Leonardson and Ripl 1980).

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Indeed, nitrogen removal from sewage has been cautioned against as a method to control eutrophication if it is likely to lower N:P ratios in downstream lakes because noxious nitrogen-fixing blue-green blooms might be enhanced (Leonardson and Bengtsson 1978; Flett et al. 1980; Smith 1983a).

Thus, if water temperature, water column stability, and light conditions are appropriate, phosphorus supply is adequate, and micronutrients like iron (Wurtsbaugh and Horne 1983) and molybdenum (Howarth and Cole 1985) do not limit nitrogen fixation, year-to-year variability in size of summer nitrogen-fixing blue-green algal blooms within an individual lake should result from differences in annual nitrogen supply. Largest blooms should be preceded by relatively low in situ nitrogen concentrations and/or low fluvial nitrogen inputs. Conversely, small blooms or years with no bloom should correlate with relatively high in situ nitrogen concentrations and/or high fluvial nitrogen loads. Our objective was to test these hypotheses at Pyramid Lake, Nevada.

Massive recurrent summer–autumn blooms of the nitrogen-fixing cyanobacterium, *Nodularia spumigena* Mertens, commonly occur in Pyramid Lake (Galat et al. 1981). Temperature does not apear to be a critical factor for *Nodularia* growth, since Cooper and Koch (1984) reported *Nodularia spumigena* blooms from April through September in nearby Walker Lake (a remnant of pluvial Lake Lahontan, as is Pyramid Lake) at water temperatures ranging from 8 to over 20°C. Internal nutrient loading via wind induced resuspension of bottom sediments is also likely to be inconsequential in this deep lake (mean depth 60 m, maximum depth 105 m). To test for a significant relationship between *Nodularia* biomass and nitrogen or phosphorus supply, we compared size of blooms with nitrogen and phosphorus concentrations and N:P ratios in Pyramid Lake prior to the July–October bloom season. We also compared bloom size with fluvial discharge, nitrogen and phosphorus mass–transport, and N:P loading ratios to the lake. Finally, we correlated bloom size with lake water specific conductance because magnitude of *Nodularia* blooms elsewhere has been shown to be influenced by differences in salinity (Lukatelich and McComb 1986).

Quantifying size of *Nodularia* blooms is difficult due to the extremely patchy spatial distribution of surface scums (Horne and Galat 1985). Landsat multispectral sensing (MSS) has been successfully used to document size and spatial heterogeneity of algal biomass (Strong 1974; Lillesand et al. 1983; Verdin 1985) and specifically *Nodularia* blooms (Oström 1976; Ulbricht and Horstmann 1980). Due to the largely cloud-free weather in the study area, archival Landsat imagery provided a technique to integrate bloom patchiness, enabling us to quantify lakewide *Nodularia* coverage approximately every 16 d between July and October for the past 15 yr.

Site Description

Pyramid Lake is a large (446 km^2), hyposaline (~5 g·L^{-1}), warm monomictic terminal lake located in the Great Basin Desert, northwestern Nevada (Galat et al. 1981). Over 90% of water influx is from the Truckee River which originates 192 km southwest as the outlet of Lake Tahoe, California. Sodium, chloride, and bicarbonate–carbonate are the principal ions contributing to its salinity. Alkalinity (~23 meq·L^{-1}) and pH (~9.2) are high and stable and thus favorable to blue-green algae (Shapiro 1984).

Like many other saline lakes (Hammer 1986), Pyramid Lake exhibits moderately high epilimnetic phosphorus concentrations (soluble reactive phosphorus (SRP) ≥50, total phosphorus (TP) ≥70 mg·m^{-3}) and low epilimnetic nitrogen concentrations (total inorganic nitrogen (TIN) ≤ 100, total nitrogen (TN) ≤1000 mg·m^{-3}) (Hamilton-Galat and Galat 1983). TIN:SRP ratios of <3:1 and TN:TP ratios of about 17:1 (by weight) are indicative of potential nitrogen deficiency (Healey and Hendzel 1980). Mean annual net primary production is moderate, ~500 mgC·m^{-2}·d^{-1}, and maximum rates occur during *Nodularia* blooms (Galat 1986).

Materials and Methods

Pyramid Lake Water Chemistry and Truckee River Nutrient Loads

Historic Pyramid Lake SRP, TP, nitrate (NO_3-N), TN (approximated as NO_3-N + total Kjeldahl nitrogen; nitrite is generally undetectable in Pyramid Lake surface water), and specific conductance were compiled for surface water samples from various sources for two seasons (Galat and Verdin 1987). Early winter holomixis (January–February, referred to as winter) was selected because nutrient concentrations and conductivity are most uniform in the water column and at highest levels before the spring growing season. The second season selected was late spring – early summer thermal stratification (May–June, referred to as spring) just before the appearance of *Nodularia* blooms, but during or subsequent to the time of highest fluvial nutrient influx. Nutrient concentrations during both intervals reflect potential supply for subsequent *Nodularia* blooms. We excluded the July–October *Nodularia* bloom season from our analysis because autochthonous nitrogen influx via fixation can be a major contributor to in situ nitrogen concentrations (Horne and Galat 1985).

Truckee River discharge to Pyramid Lake was gathered from U.S. Geological Survey records at the Nixon, Nevada, stream gage located 21 km upstream from Pyramid Lake (U.S. Geological Survey 1972–1986). Nutrient concentrations used to estimate loadings were compiled from one to five samples per month from three agencies monitoring Truckee River water quality near Nixon between 1973 and 1986. Phosphorus and nitrogen fractions included were SRP, TP, TIN (sum of ammonia, nitrite, and nitrate), and TN (sum of nitrite, nitrate, and Kjeldahl nitrogen). Locations of collection sites, methods of collection, and analytical procedures differed somewhat among agencies and are available from the authors on request (Galat and Verdin 1987).

Several techniques were evaluated to calculate annual mass-transport of Truckee River nutrients to Pyramid Lake (D. Galat, unpubl. data). Due to the lack of a statistical dependence of nutrient concentration on discharge, we calculated monthly mass-discharge as the product of monthly mean flow-weighted concentration and monthly total discharge (Yaksich and Verhoff 1983). Monthly nutrient loads calculated in this manner were summed for November–October to yield "annual" loads to Pyramid Lake for the 12 mo preceding and encompassing the July–October *Nodularia* bloom season. Annual loads were converted from tonnes per year to milligrams per square metre per year to normalize for differences in lake surface area among years.

Landsat Image Analysis

Landsat MSS band 3 (700–800 nm wavelength) film negatives were obtained for the July–October *Nodularia* bloom season from 1972 through 1986. Penetration depth of solar radiation detectable by band 3 at these wavelengths is about 1 m, and therefore, coverage in this study was restricted to surface and near-surface conditions. Vertical profiles of *Nodularia* biomass, nitrogen fixation, and photosynthesis in Pyramid Lake (Horne and Galat 1985; Galat 1986) and density and nitrogen fixation in the Baltic Sea (Lindahl et al. 1980; Rinne et al. 1981) and the Peel–Harvey Estuary, Western Australia (Huber 1986), indicate that *Nodularia* is concentrated at the surface due to its positive buoyancy. Occasionally, wind-induced turbulence will mix a significant fraction of *Nodularia* biomass below the maximum depth of Landsat registration, and in these instances, bloom size will be underestimated using Landsat imagery (D. L. Galat and J. P. Verdin, in prep.).

Techniques used to process film negatives and convert film negative density to chlorophyll *a* are detailed in Galat and Verdin (1987) and will only be summarized here. A subset of each negative including Pyramid Lake was redigitized using a scanning microdensitometer, and the density histograms produced were normalized across all dates for differences in photo lab procedures, sun angle, and atmospheric effects. Images were spatially registered and land masked out by sorting into five groups based on differences in lake surface area over the 15 yr. Each image falling within a group was registered to the pixel grid of the master for its group using 10 shoreline features as control points, a first-order coordinate conversion, and a nearest-neighbor resampling algorithm (Lillesand and Kiefer 1987). To compensate in part for the lower radiometric accuracy of digital data generated from film negatives rather than computer tapes, image data were low pass filtered by passing a 3×3 median window over them to replace noise pixels with values more representative of the water mass as a whole (Lillesand and Kiefer 1987).

A 32-site surface water chlorophyll synoptic survey was conducted during the 1986 *Nodularia* bloom concurrent with a flyby of Landsat 5. At each site, five surface to 0.5-m depth integrated water samples were collected along a 10-m transect to integrate mesoscale surface variability. Samples were pooled and replicate subsamples removed for chlorophyll *a* analysis. Filtration, grinding, acetone extraction, centrifuging, and spectrophotometric measurement of chlorophyll *a* corrected for pheophytin degradation followed APHA et al. (1985) procedures. Both the Landsat digital tape and MSS band 3 film negative for the synoptic survey were acquired, and regressions were calculated to predict (1) surface water chlorophyll *a* from tape radiance and (2) tape radiance from film density. This enabled us to convert lakewide mean film density from Landsat film negatives to surface water *Nodularia* biomass expressed as chlorophyll *a*.

Surface water chlorophyll *a* was predicted from the 1986 synoptic survey and MSS band 3 tape radiances by pairing observed chlorophyll *a* concentrations from the synoptic survey with corresponding tape radiance values from equivalent cumulative frequencies along the cumulative frequency distributions of both variables. The following regression equation was calculated for estimating surface water chlorophyll *a* concentration from tape radiance counts:

$$(1)\quad \mathrm{CHL} = -14.533 + 4.493\,(\mathrm{TRC})$$
$$(R^2 = 0.951,\ P \leq 0.001,\ N = 27)$$

where CHL is surface water chlorophyll *a* concentration (milligrams per cubic metre) and TRC is Landsat 5, MSS band 3 tape radiance counts. To derive a relationship between tape image radiance and scanned film density, a scene subset of the scanned film negative was matched by coordinate transformation to the same subset in the band 3 tape image for the 20 July 1986 scene. Cumulative histograms were prepared and equivalent points at 5% intervals along the histograms paired to provide input into the regression procedure. The calculated regression was

$$(2)\quad \ln \mathrm{TRC} = 1.787 + 0.015(\mathrm{FDC})$$
$$(R^2 = 0.995,\ P \leq 0.001,\ N = 17)$$

where FDC is film density count and TRC is the corresponding band 3 tape radiance count. Equation (2) was used to convert film density values from archival Landsat film negatives to tape radiances. Mean tape radiance for each of the 84 usable 1972–86 Pyramid Lake scenes was then calculated and converted to mean surface water chlorophyll *a* using regression model (1).

Each Landsat film negative was visually examined and compared with historic information on Truckee River discharge and Pyramid Lake limnology. Images where surface radiance showed patterns characteristic of suspended sediment or calcium carbonate from whitings and subsequently corroborated by high fluvial discharge (U.S. Geological Survey 1972–1986) or a verified whiting (Galat and Jacobsen 1985) at the time of Landsat overpasses were not included in subsequent analyses. The image with the highest predicted mean chlorophyll *a* concentration among all available Landsat scenes between July and October for each year was defined as the maximum mean surface water chlorophyll *a* concentration (MMCHL) for that year. These values were tested against the corresponding year's data for Pyramid Lake nutrient chemistry and conductivity and Truckee River annual discharge and nutrient loads to Pyramid Lake. Pairwise Pearson univariate correlation coefficients were calculated between MMCHL and these variables. Those that exhibited significant univariate correlations with MMCHL ($P \leq 0.05$) and were demonstrated free of significant intercorrelations with other independent variables ($P > 0.05$) were tested against MMCHL by univariate or stepwise multivariate linear regression.

Results

Pyramid Lake Water Chemistry and Truckee River Discharge and Nutrient Loads

Surface water nutrient concentrations and specific conductance information for either early winter holomixis or late spring – early summer stratification were available for 9 of the 15 yr between 1972 and 1986. Data for both winter and spring were present for 6 yr: 1976, 1977, 1979, 1983, 1984, and 1986. Nutrient concentrations and conductivity during spring across these years were significantly lower than during winter for NO_3-N and NO_3-N:SRP ratios, but there were no significant differences between seasons for SRP, TP, and conductivity (Wilcoxon signed rank test, Table 1). Insufficient data from both seasons were available to make similar comparisons for TN. Two distinct groups emerged when water chemistry data were compared among the 6 yr: Group 1 (1976, 1977, 1979) and Group 2 (1983, 1984, 1986). Surface water concentrations of nitrogen and phosphorus during both seasons and NO_3-N:SRP ratios and conductivity during spring were significantly lower for Group 2 years than Group 1 years (Mann–Whitney test, Table 1).

TABLE 1. Means and standard deviations (SD) for Pyramid Lake surface water chemistry at early winter holomixis (W) and early summer stratification (S) for two groups of years. Wilcoxin signed rank test was used to compare seasons across years and Mann–Whitney test was used to compare year groups for each season. NS, $P > 0.05$; *$P \leq 0.05$.

		Group 1 (1976, 1977, 1979)		Seasons, groups combined	Groups, seasons separate	Group 2 (1983, 1984, 1986)	
Parameter	Season	Mean	SD			Mean	SD
SRP	W	90	0	NS	*	53	14
($mg \cdot m^{-3}$)	S	83	15		*	44	15
TP	W	103	6	NS	*	61	9
($mg \cdot m^{-3}$)	S	102	8		*	61	9
NO_3-N	W	70	20	*	*	24	20
($mg \cdot m^{-3}$)	S	40	17		*	3	2
NO_3-N:SRP	W	1.7	0.5	*	NS	1.0	0.8
	S	0.8	0.5		*	0.1	0.1
Conductivity	W	8.3	0.2	NS	NS	8.0	0.4
($mS \cdot cm^{-1}$)	S	8.5	0.1		*	7.6	0.5

TABLE 2. Summary of November–October Truckee River discharge and loads of soluble reactive phosphorus (SRP), total phosphorus (TP), total inorganic nitrogen (TIN), total nitrogen (TN), and TN:TP loading ratios to Pyramid Lake, 1972–86. Nutrient loads were not calculated for years with <7 mo of data. Corresponding maximum mean chlorophyll *a* concentrations (MMCHL) between July and October for each year were predicted from Landsat imagery.

		Projected loads to Pyramid Lake						
		$mg \cdot m^{-2} \cdot yr^{-1}$					MMCHL	
Year	Discharge (Mm^3)	SRP	TP	TIN	TN	TN:TP	$mg \cdot m^3$	Date
1971–72	238.4	—	—	—	—	—	31	25 July
1972–73	440.9	206	365	650	1231	3.4	30	2 July
1973–74	860.0	309	420	812	1596	3.8	47	2 Aug.
1974–75	680.3	259	345	574	1799	5.2	39	11 Sept.
1975–76	337.5	198	233	509	929	4.0	30	5 Sept.
1976–77	48.2	24	28	62	126	4.6	45	31 Aug.
1977–78	129.0	21	56	95	367	6.5	28	19 Oct.
1978–79	107.5	33	77	150	333	4.3	49	17 Sept.
1979–80	504.4	194	320	662	1498	4.7	28	8 Oct.
1980–81	187.6	84	123	257	567	4.6	35	10 Aug.
1981–82	1202.1	157	434	1316	3689	8.5	30	5 Oct.
1982–83	2292.6	164	882	2141	—	—	31	21 Aug.
1983–84	1379.1	83	412	951	2022	4.9	56	14 July
1984–85	295.5	22	77	416	778	10.1	41	1 July
1985–86	1226.3	127	517	1229	3775	7.3	72	20 July

TABLE 3. Pearson correlation matrix for November–October 1972–86 Truckee River discharge (log Q), soluble reactive phosphorus (SRP), total phosphorus (TP), total inorganic nitrogen (TIN), total nitrogen (TN) loads, TN:TP loading ratios to Pyramid Lake, and Landsat-predicted Pyramid Lake maximum mean chlorophyll *a* concentrations (MMCHL) and log Q. *$P \leq 0.05$; **$P \leq 0.01$.

	MMCHL	log Q	SRP	TP	TIN	TN	TN:TP
MMCHL	—	0.175	−0.154	0.083	0.076	0.379	0.085
log Q	—	—	0.580*	0.898**	0.888**	0.849**	0.186

November through October Truckee River discharge varied from 48 (1976–77) to 2293 Mm^3 (1982–83) (and averaged 662 $Mm^3 \pm 126$ SE over the 15 yr. Lowest discharges were recorded for the 3 yr between November 1976 and October 1979, and highest discharges were observed between November 1981 and October 1984 and also November 1985 through October 1986 (Table 2). Not surprisingly, annual loads for all nutrient fractions showed significant positive correlations with discharge (Table 3). Comparing November–October Truckee River discharge and nutrient flux to Pyramid Lake between the two groups previously defined illustrates that low fluvial discharge occurred in Group 1 years, while years in Group 2

TABLE 4. Means and standard deviations (SD) for November–October Truckee River discharge (Mm^3), soluble reactive phosphorus (SRP), total phosphorus (TP), and total inorganic nitrogen (TIN) loads ($mg \cdot m^{-2}$) to Pyramid Lake. Mann–Whitney test was used to test for significant differences between groups of years. NS, $P > 0.05$; $^*P \leq 0.05$.

	Group 1 (1976, 1977, 1979)		Significance	Group 2 (1983, 1984, 1986)	
Parameter	Mean	SD	level	Mean	SD
Discharge	164.4	152.8	*	1632.7	576.6
SRP	85	98	NS	90	71
TP	113	107	*	604	247
TIN	240	237	*	1440	623

were characterized by high discharge and nutrient loads. Higher Truckee River discharge, TP, and TIN loads entered Pyramid Lake during Group 2 years than during Group 1 years (Mann–Whitney test, Table 4). Fluvial TN import was also much greater during 1984 and 1986 than in Group 1 years (Table 2). However, sample sizes were too small (TN loads were not measured in 1983) to permit statistical comparisons between the two groups of years. Only flux of SRP did not change significantly between the two periods. Improved removal of phosphorus from wastewater by the cities of Reno and Sparks, Nevada (~92 km upstream from Pyramid Lake) was implemented in 1982 and probably accounts for this result.

Correlations were also calculated between Truckee River discharge and nutrient loads to Pyramid Lake and lake surface water nutrient concentrations for winter and spring from corresponding years. The only significant correlations ($P \leq 0.05$) were between November–October fluvial discharge and spring lake water levels of TP ($r = -0.876$) and NO_3-N ($r = -0.765$). Although nutrient import from rivers is often positively associated with nutrient levels in receiving waters, there were no significant correlations ($P > 0.05$) between inputs to Pyramid Lake of Truckee River nutrients and winter or spring surface water concentrations of their counterparts in the lake. To summarize, late spring – early summer TP and nitrate concentrations in lake surface water were significantly lower during years of very high Truckee River discharge than during years of very low discharge, even though large quantities of these nutrients were imported to the lake in winter and spring by high river discharge.

This anomaly was a result of record high Truckee River discharges during 1982, 1983, 1984, and 1986 which raised the surface elevation of Pyramid Lake 9.0 m and increased its volume by 16% (U.S. Geological Survey 1972–1986). Annual discharge from 1982 to 1984 ranged from two to over five times higher than the previous 20 yr average of about 400 Mm^3, and based on tree-ring indices for northeastern Nevada, 1983 and 1984 were the wettest 2 yr since at least 1600 (W. P. Smith 1986). The effect on nutrient dynamics in Pyramid Lake of this unprecedented freshwater influx is illustrated by examining 4 yr when comparative limnological data were available, 2 yr of very low river discharge (1977, 1979), and also 2 yr when discharge was very high (1984, 1986). The large volume of freshwater (<200 $\mu S \cdot cm^{-1}$ conductivity) entering Pyramid Lake did not completely mix with the underlying saline lake water and produced temporary ectogenic meromixis (sensu Walker and Likens 1975). Figure 1 illustrates typical isohaline conductivity profiles for early June 1977 and late June 1979. Summer thermal stratification was only weakly developed and deepwater oxygen

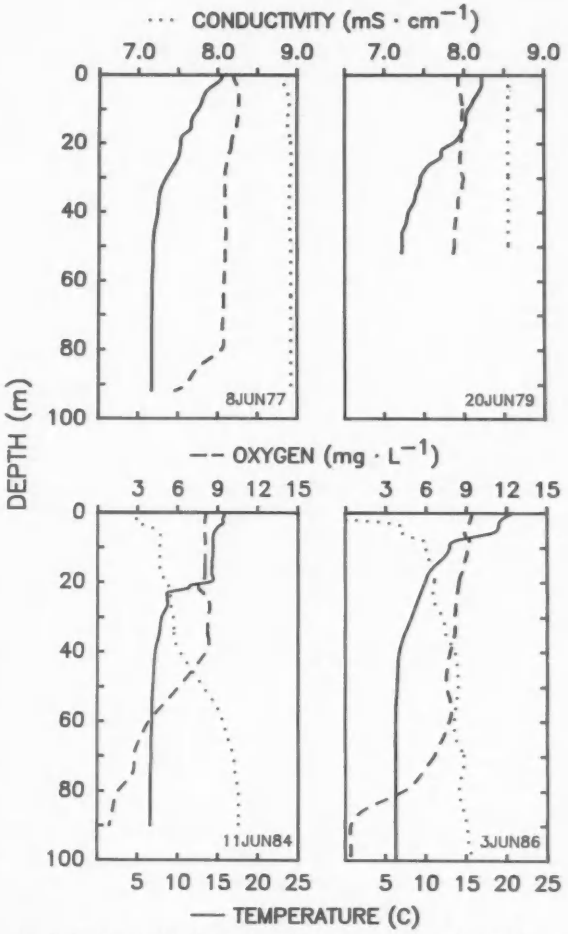

FIG. 1. Surface to lake bottom profiles of temperature, dissolved oxygen, and specific conductance during early summer thermal stratification in Pyramid Lake.

concentrations were greater than 6.0 $mg \cdot L^{-1}$. Profiles were much different at similar times in 1984 and 1986. Conductivity increased noticeably with depth, thermal stratification was well developed by mid-June, indicating greater vertical stability, and hypolimnetic (monimolimnetic) oxygen concentrations were less than 6.0 $mg \cdot L^{-1}$ below 50-m depth in 1984 and below 75-m depth in 1986. Without complete winter–spring circulation, hypolimnetic nutrients were not relocated to the euphotic region for assimilation by phytoplankton. This resulted in unusually high June 1984 and 1986 bottom water TP (also SRP) and TIN concentrations, but lower surface water concentrations than were measured in 1977 or 1979 (Fig. 2).

Chlorophyll *a* During *Nodularia spumigena* Blooms and Comparisons with Nutrient Supply

July–October mean surface water chlorophyll *a* concentrations estimated from Landsat images ranged from 27.5 to 72.0 $mg \cdot m^{-3}$ with an average coefficient of variation about the mean on individual dates of 32%. Mean predicted lakewide chlorophyll *a* concentrations seldom exceeded 30 $mg \cdot m^{-3}$,

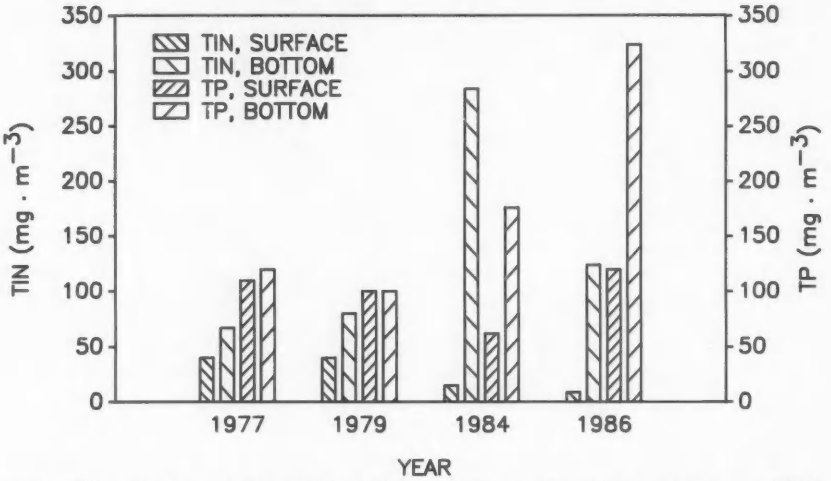

FIG. 2. Differences between Pyramid Lake surface and bottom water, total inorganic nitrogen (TIN), and total phosphorus (TP) for years of low (1977, 1979) and high (1984, 1986) Truckee River discharge. Dates of profiles are 20 May 1977, 15 May 1979, 11 June 1984, and 5 May 1986.

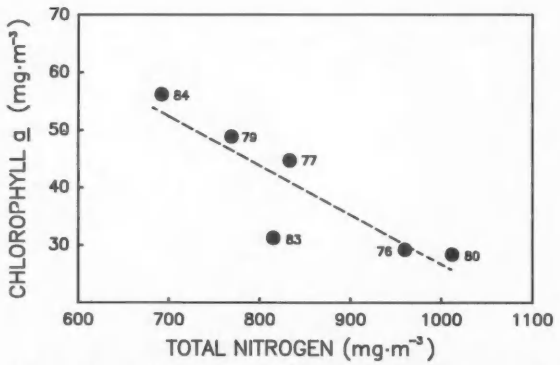

FIG. 3. Relationship between Pyramid Lake surface water total nitrogen during early winter holomixis and predicted maximum mean chlorophyll *a* concentrations during the summer–autumn *Nodularia* bloom season ($R^2 = 0.76$, $P = 0.02$). Numbers within figure axes are years for which data were available.

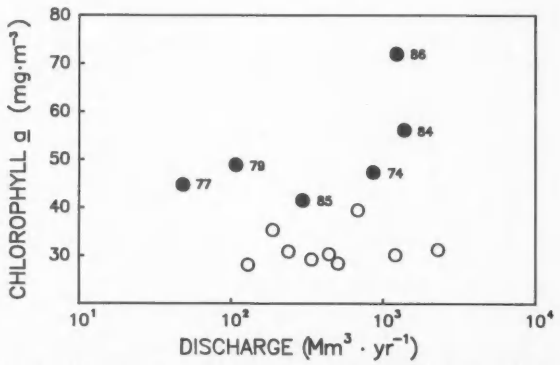

FIG. 4. November–October Truckee River discharge to Pyramid Lake (log transformed) plotted against predicted maximum mean chlorophyll *a* concentrations in Pyramid Lake surface water during the summer–autumn *Nodularia* bloom season ($R^2 = 0.03$, $P = 0.52$). Numbers and filled circles refer to years when very large *Nodularia* blooms (>40 mg chlorophyll $a \cdot m^{-3}$) were observed.

except during *Nodularia* blooms. "Very large" blooms, defined here as predicted mean surface water chlorophyll *a* concentrations >40.0 $mg \cdot m^{-3}$, were recorded in 1974, 1977, 1979, 1984, 1985, and 1986. Although size of blooms was quite variable among years, years without noticeable *Nodularia* blooms were uncommon (1973, 1980, 1982).

TN concentration during winter was the only lake chemistry variable significantly correlated with MMCHL during any season ($r = -0.872$, $P \leq 0.05$). The univariate regression of MMCHL on TN was

$$\text{MMCHL} = 112.468 - 0.086[\text{TN}]$$
$$(P = 0.023, N = 6).$$

This regression accounted for 76% of the observed variance in MMCHL and indicates that *Nodularia* blooms were generally largest in years when surface water TN concentrations during early winter were lowest (<850 $mg \cdot m^{-3}$, Fig. 3).

Correlation coefficients between TP, SRP, NO_3-N, and conductivity and the dependent variable MMCHL were not significant ($P > 0.05$). Very large summer–autumn *Nodularia* blooms were recorded subsequent to wide ranges of spring surface water constituents: TP, 40–100 $mg \cdot m^{-3}$; SRP, 30–70 $mg \cdot m^{-3}$; NO_3-N, <2–50 $mg \cdot m^{-3}$; SRP:NO_3-N, <0.1–0.7 (weight); TN:TP, 7–15 ·(weight); and conductivity, 7.2–8.6 $mS \cdot cm^{-1}$. Furthermore, there were also no significant correlations between November–October Truckee River discharge, SRP, TP, TIN, and TN loads or TN:TP loading ratios to Pyramid Lake and MMCHL. Because fluvial loadings of all nutrients were significantly correlated with Truckee River discharge (Table 3), we graphed MMCHL against discharge to examine their interactions (Fig. 4). Although high MMCHL concentrations (MMCHL≥40 $mg \cdot m^{-3}$) characteristic of very large *Nodularia* blooms occurred over the entire range of Truckee River discharge and nutrient loads (Fig. 4), they predominated at extremes of discharge and nutrient influx: very high discharges (>1000 Mm^3 in 1974, 1984, 1986) and also very low discharges (<110 Mm^3 in 1977, 1979). Low MMCHL concentra-

tions (<40 mg·m^{-3}) were never recorded in years of very low Truckee River discharge or nitrogen and phosphorus loads, but were observed when discharge and nutrient loads were intermediate to high (Table 2; Fig. 4).

Discussion

Analysis of 15 yr of Landsat data was an effective approach to document relative magnitude and frequency of blue-green algal blooms in Pyramid Lake. Frequent summer–autumn dominance by blue-green algae in this desert saline lake is consistent with evidence from freshwater lakes also exhibiting low epilimnetic TN:TP ratios (Smith 1983a). Lack of a correlation between maximum biomass of *Nodularia* blooms and the range of winter TN:TP ratios in Pyramid Lake (16–26) is not surprising, however, as no clear pattern of blue-green dominance was observed by Smith (1983a, 1983b) when TN:TP ratios were <29:1. Ratios of TN:TP do not appear to be useful predictors of blue-green algal dominance within a single lake unless the range of their interannual variability is great. Presence of heterocystous *Nodularia* in Pyramid Lake is also consistent with the prediction of Flett et al. (1980) that nitrogen-fixing blue-green algae are associated with waters having external TN:TP loading ratios <10. Nevertheless, fluvial TN:TP loading ratios over the range observed for Pyramid Lake (3.4–10.1) also were not good predictors of size of *Nodularia* blooms. If one accepts magnitude of *Nodularia* blooms estimated from Landsat imagery as an index of the relative magnitude of nitrogen fixation in Pyramid Lake (cf. Oström 1976; Horne and Galat 1985), then our results are in agreement with those of Toetz and McFarland (1987), who were unable to demonstrate a proposed negative relationship between magnitude of nitrogen fixation and TN:TP ratios of loadings to lakes. Equivocal results from the present study and others cited suggest caution against overinterpretation of results from empirical studies showing high correlations between N:P ratios and biomass or nitrogen fixation of blue-green algal blooms. It is not the ratio of the two nutrients per se, but the relative supply rate of each that stimulates growth or enzymatic nitrogen fixation.

There were no significant correlations between lake water phosphorus concentrations preceding the *Nodularia* bloom season or influx of Truckee River phosphorus and size of subsequent *Nodularia* blooms. This lack of association would be anticipated if phosphorus supply were in excess of demand. Huber and Hamel (1985a) documented a massive *Nodularia spumigena* bloom in Peel–Harvey Estuary, Western Australia, during which SRP concentrations were always <15 mg·m^{-3}. Their laboratory experiments showed a negligible increase in *Nodularia* biomass in cultures beyond 50 mg added phosphorus·m^{-3}. Moreover, *Nodularia* transferred from phosphorus-complete to phosphorus-free medium was able to grow for 6 d at a rate similar to *Nodularia* in phosphorus-complete medium (Huber and Hamel 1985b). *Nodularia* maintained these high growth rates under SRP-starved conditions by production of alkaline phosphatase. SRP concentrations in Pyramid Lake preceding *Nodularia* blooms were never <30 mg·m^{-3}. Recent evidence suggests that pre-1986 SRP concentrations measured at Pyramid Lake are artificially high, by as much as 14%, due to lack of correction for arsenate interference (Williamson and Horne 1986), and therefore, a more conservative prebloom minimum SRP estimate might be 20 mg·m^{-3}. Huber and Hamel's (1985a, 1985b) evidence and results from our study imply that phosphorus does not presently limit size of *Nodularia* blooms in Pyramid Lake.

Summer–autumn *Nodularia* blooms in Pyramid Lake were negatively associated with surface water total nitrogen concentrations during winter circulation as hypothesized by us and others (DePinto et al. 1976; Schindler 1977; but see Smith 1983b; Trimbee and Prepas 1987). Nevertheless, largest *Nodularia* blooms occurred under two very different hydrologic circumstances, segregating into the two groups described earlier. The 1977 and 1979 blooms were in years of extremely low Truckee River discharge and peaked from late August to mid-September. Very large *Nodularia* blooms in 1974 and 1984–86 were either in or followed years of above-average Truckee River discharge and generally peaked in July.

The very large 1977 and 1979 blooms were preceded by low surface water concentrations of nitrogen, high phosphorus levels (Table 1), and low import of Truckee River nitrogen (Table 4). These data support the prevailing view that large blue-green blooms appear when lake water phosphorus levels are high, nitrogen is low (i.e. low N:P ratios), and fluvial nitrogen loads are also low. The very large 1984 and 1986 blooms were also preceded by low lake water inorganic nitrogen concentrations and moderate phosphorus levels, and N:P ratios remained indicative of nitrogen deficiency. However, there was a large influx of fluvial nitrogen in contrast with 1977 and 1979, but this was not reflected in higher vernal surface water concentrations of nitrogen, smaller *Nodularia* blooms as predicted, or a delay in bloom onset. The cause for these differences appears to be temporary meromixis induced by the large influx of river water transporting this nitrogen. We argue that the vernal pulse of diatoms and green algae, characteristic of Pyramid Lake (Galat et al. 1981; Galat 1986), was more dependent on fluvial nitrogen and phosphorus import from 1982 to 1986 because meromixis reduced vertical mixing and entrained a large fraction of the internal nutrient pool in the monimolimnion. Failure of normally monomictic Pyramid Lake to undergo complete winter circulation prompted earlier stable summer thermal stratification. This is an expected consequence of reducing the annual heat budget by decreasing the volume of lake water participating in overturn. Early summer thermal stratification resulted in earlier depletion of surface water nitrogen and phosphorus by phytoplankton uptake and the subsequent early appearance of *Nodularia* blooms in 1984 and 1986. This scenario is consistent with the negative correlation observed between winter lake water TN concentrations and size of *Nodularia* blooms, although as we suggest, the causal mechanisms responsible for low nitrogen concentrations differed among years.

Long-term trends of *Nodularia* blooms in a saline desert lake support the paradigm of blue-green algal dominance in phosphorus-rich, nitrogen-poor systems developed largely from temperate lakes in mesic climates. Nevertheless, variations in size of *Nodularia* blooms at Pyramid Lake demonstrate the importance of climatic forcing on allogenic processes and subsequent availability of nutrients for phytoplankton growth and succession. Temporary meromixis, by reducing nitrogen supply to the euphotic zone, fortuitously provided us with a natural whole-lake manipulation experiment and corroborated the hypothesized relationship between nitrogen limitation and blue-green algal blooms. Analysis of long-term nutrient data and use of archival remote sensing was an approach intended to incorporate temporal variability as an asset to test hypotheses about nutrient control of blue-green algal blooms. Planned nutrient manipulation experiments and before-and-after monitoring of

how changes in wastewater nutrient removal programs influence receiving lakes are also needed if the largely untested predictions about size of blue-green algal blooms and the N:P ratio concept are to be critically evaluated.

Saline lakes comprise nearly one half the earth's total lake volume (Wetzel 1983) and they often occur in desert regions where nitrogen also limits terrestrial plant productivity (West and Klemmedson 1978; Hadley and Szarek 1981). Sparse terrestrial plant biomass, low decomposition rates, and low leaching rates in xeric, compared with mesic, climates result in low allochthonous organic matter transport to lakes (Galat 1986). The amount of terrestrial nitrogen flux to desert waters is, therefore, also lessened. Additionally, high rates of erosion from sparsely vegetated soils in semiarid and arid regions transport relatively large quantities of phosphorus to rivers and lakes (Goldman and Horne 1983), while lack of outlets from most saline lakes eliminates fluvial phosphorus efflux. We propose, therefore, that desert saline lakes, like many desert streams (Grimm and Fisher 1986), are potentially nitrogen limited. Fixation by *Nodularia* has been shown to be a major vector of nitrogen to Pyramid Lake (Horne and Galat 1985), and in this sense the lake is analogous to the adjacent terrestrial desert where fixation by blue-green algae is also a major source of autochthonous nitrogen (Rychert et al. 1978; Ghabbour et al. 1980). We anticipate that other waters in arid climates may also be relatively rich in phosphorus and poor in nitrogen and therefore fruitful locations to test hypotheses of mechanisms controlling blue-green algal dominance and their role as a nitrogen source for seasonal succession to other algae.

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Distribution and Abundance of the Toxic Dinoflagellate *Gonyaulax excavata* in the Bay of Fundy

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Martin, J. L., and A. W. White. 1988. Distribution and abundance of the dinoflagellate *Gonyaulax excavata* in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 45: 1968–1975.

Water samples were collected for five consecutive summers (1980–84) in the Bay of Fundy at the surface and at 5 m to examine the distribution patterns of the motile stages of the toxic dinoflagellate *Gonyaulax excavata*, which has caused shellfish toxicity in this area for years, as well as occasional fish kills. In 1980 and 1981, 128 and 122 stations were sampled, respectively, and 84 and 41% of the samples contained *G. excavata* cells. Further sampling in 1982–84 was reduced to areas where most cells were observed in previous years. During this period, *G. excavata* was observed in 91–100% of the locations sampled. Despite variations in abundance of *G. excavata* cells from year to year, the overall distribution patterns were similar. The highest concentrations of cells occurred in the south-central and southwestern portions of the Bay in the area bounded by the Quoddy Region and Saint John, New Brunswick, and Digby, Nova Scotia. The distribution of various life cycle stages (planozygotes, vegetative duplets, and sexually fusing cells) was similar to that of individual motile cells, suggesting that the annual blooms in this region behave as one large population. Few or no *G. excavata* cells were found at the head of the Bay or at the seaward approaches. Results suggest the prevailing circulation in the Bay and the presence of tidal fronts are dominant factors in retaining *G. excavata* and its life cycle stages in the south-central and southwestern portion of the Bay and that this accounts for its perennial occurrence in this area.

Des échantillons d'eau ont été prélevés pendant cinq étés consécutifs (1980–1984) dans la baie de Fundy. Les échantillons, prélevés en surface et à 5 m de profondeur, ont servi à étudier les allures de la répartition des stades motiles du dinoflagellé toxique *Gonyaulax excavata* qui, pendant plusieurs années, a rendu les mollusques toxiques et, à l'occasion, provoqué des hécatombes de poissons dans cette région. En 1980 et 1981, respectivement 128 et 122 stations ont été échantillonnées. Des échantillons prélevés, 84 et 41 % contenaient des cellules de *G. excavata*. D'autres prélèvements ont été réalisés de 1982 à 1984 dans les zones où les plus grandes quantités de cellules avaient été décelées les années précédentes. Au cours de cette période, des *G. excavata* ont été découverts dans 91–100 % des endroits examinés. En dépit des variations annuelles de l'abondance des cellules de *G. excavata*, les modes de répartition généraux demeuraient semblables. Les concentrations les plus élevées ont été notées dans la partie centre-sud et sud-ouest de la baie, dans la zone se trouvant entre la région de Quoddy et Saint-Jean (Nouveau-Brunswick), et Digby (Nouvelle-Écosse). La distribution des cellules aux divers stades (planozygotes, doublets végétatifs et cellules en fusion sexuelle) était semblable à celle des cellules motiles individuelles, ce qui porte à croire que les individus qui pullulent annuellement dans cette région se comportent comme faisant partie d'une grande population. Peu ou pas de cellules de *G. excavata* ont été décelées dans le fond de la baie ou à son embouchure. Les résultats obtenus portent à croire que la circulation principale de la baie et la présence de fronts de marée sont les facteurs dominants qui retiennent *G. excavata*, à tous les stades de développement, dans la partie centre-sud et sud-ouest de la baie et en expliquent la persistance à cet endroit.

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The toxic marine dinoflagellate *Gonyaulax excavata*[2] (= *G. tamarensis* var. *excavata*) is responsible for paralytic shellfish poisoning (PSP, a potentially fatal food poisoning) on Canada's east coast. Blooms of this dinoflagellate are an annual occurrence in the Bay of Fundy and the St. Lawrence estuary. Shellfish toxicity records from the Bay of Fundy date to 1935 showing evidence of molluscan shellfish accumulating paralytic shellfish poisons while filter feeding, causing PSP in humans and other vertebrates when ingested. Fish kills can also result from toxin transfer through the food web during intense blooms (White 1980, 1982, 1984).

Soft-shell clams (*Mya arenaria*) have been harvested in the Bay of Fundy for years with an annual seasonal closure due to unacceptable levels of paralytic shellfish toxins. Blue mussel (*Mytilus edulis*) harvesting has been prohibited in the entire Bay of Fundy for many years because of high toxin levels.

Gonyaulax excavata usually reproduces by means of asexual division, but a sexual phase can occur when gametes are formed that fuse to form a motile zygote or "hypnozygote." This large hypnozygote swims for a few days before developing into a cyst and settling to the bottom. This benthic resting cyst overwinters in the upper layers of sediment until a rise in water temperature induces germination to excystment into a vegetative cell

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[2]Taxonomy of this organism is in flux and the acceptable nomenclature is *Gonyaulax*, *Protogonyaulax*, or *Alexandrium*.

(Anderson 1980). Initially, newly excysted cells develop into large swimming cells or "planomeiocytes" which divide to produce vegetative cells.

During the winter of 1980–81, an extensive sampling survey of bottom sediments throughout the Bay of Fundy indicated *G. excavata* cysts present in low to moderate numbers in most offshore and intertidal areas. A rich deposit of cysts was found east and north of Grand Manan Island (White and Lewis 1982). This region of the Bay of Fundy serves as a major depositional area for silt/clay sediments and cysts. The results of this 5-yr survey on abundance and distribution of *G. excavata* and its major life cycle stages in the surface waters are discussed in relation to this natural cyst reservoir. Prior to our work, little was known of the patterns and distribution of *G. excavata* motile cells and their variation from year to year in the Bay of Fundy, thus prompting this survey to be initiated. The annual pattern of distribution is also discussed in relation to the retention mechanism provided by the circulation patterns and frontal regions within the Bay of Fundy.

Materials and Methods

Sampling

Plankton samples were collected for determination of *G. excavata* distribution and abundance throughout the Bay of Fundy for 5 consecutive yr. Sampling dates were August 14–20, 1980; July 31 – August 10, 1981; August 3–12, 1982; July 26–29, 1983; and July 10–26, 1984. Stations sampled are shown in Fig. 1. Sampling periods were determined by weekly monitoring of a sampling station off Campobello Island, a review of previous shellfish and toxicity records, and availability of ship time. Sampling areas varied from year to year as shown in Fig. 2.

An extensive surface water survey in 1980 and 1981 included the approaches as well as the entire Bay of Fundy, with 128 and 122 stations sampled, respectively (Fig. 2). Subsequent sampling in 1982 was reduced to 85 stations (Fig. 2). Sampling during 1983 and 1984 was limited to 55 and 43 locations, respectively (Fig. 2), where highest concentrations of cells had been observed in previous years. Samples at these locations were taken from the surface and a depth of 5 m to determine variability in cell abundance for the two depths. The water was sampled regardless of time of day for the years 1980, 1981, and 1983 whereas samples were collected only between 0700 and 2300 in 1982 and 1984.

Water was collected by bucket at the surface and 1.25-L Nansen bottle at 5 m for determination of temperature, salinity, and *G. excavata* abundance. The samples for *G. excavata* abundance were immediately preserved with 2.5% formalin – acetic acid (1:1) and subsequently a 50-mL subsample from each sample was settled in a chamber for counting with an inverted microscope. All plankton was identified, with *Gonyaulax* counts including all life cycle stages present. Reproduction of *G. excavata* is by asexual division of gametes forming duplets. As a bloom progresses, sexual fusing of gametes occurs, yielding a swimming zygote (planozygote) which becomes a nonmotile resting cyst or hypnozygote (Anderson and Wall 1978; Turpin et al. 1978; Anderson 1980). Fusing cells were distinguished from asexually dividing cells by the cingula of the fusing cells being at oblique angles to each other whereas the cingula of duplets are parallel. Planozygotes, fused gametes, duplets, triplets, quadruplets, and hypnozygotes were differentiated for all years excluding 1980 in which only total *Gonyaulax* numbers were recorded. Planozygotes were those cells with a length greater than or equal to 43 μm and differed from planomeiocytes in an absence of the characteristic red pigment of a newly germinated cell. All cysts identified in this study were newly formed in that they were completely filled with starch or lipid reserves.

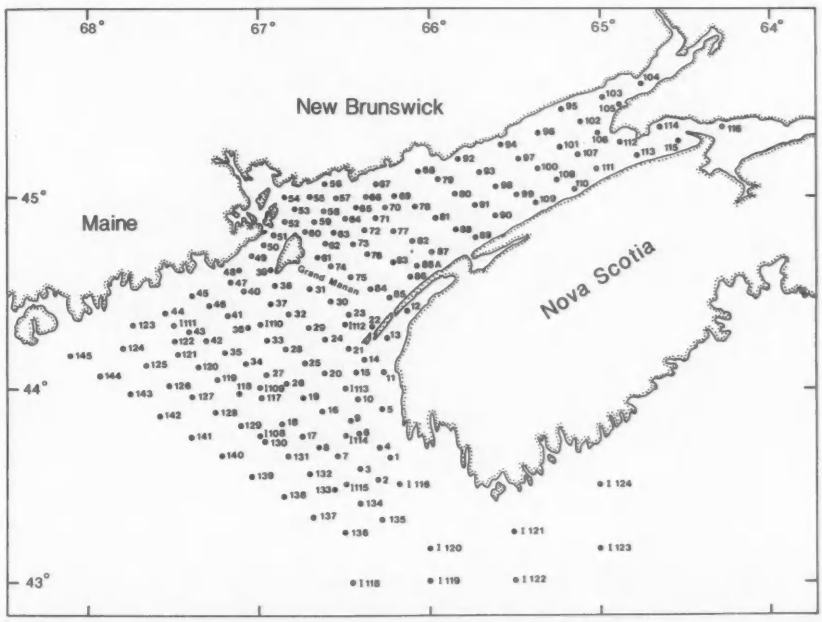


FIG. 1. Locations of sampling stations in the Bay of Fundy area.

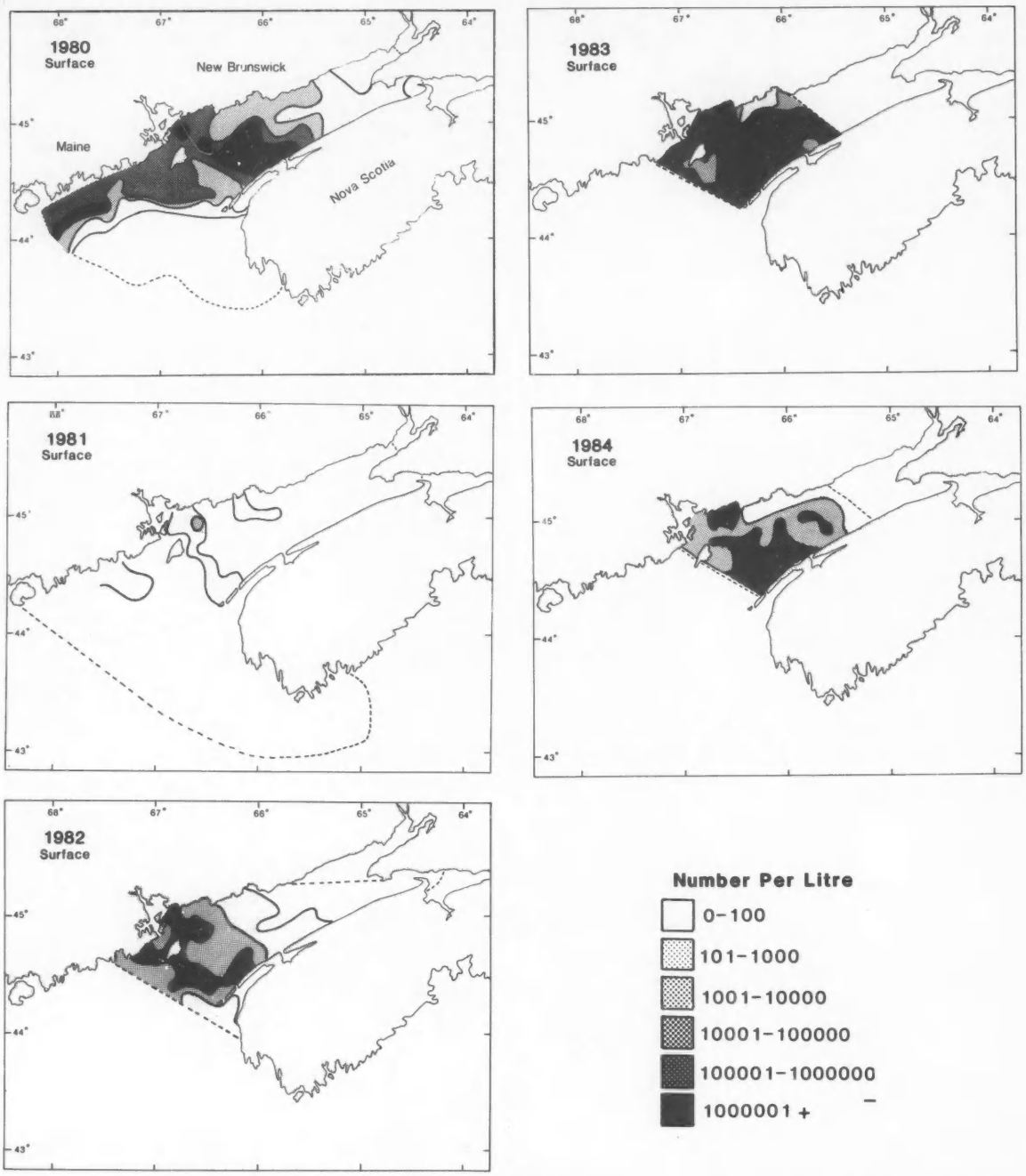


FIG. 2. Surface concentrations of *G. excavata* motile cells through the five sampling periods, 1980–84. Broken lines indicate outer limits of areas sampled.

Salinity was analyzed using a Guildline Instruments Limicea model 8400 salinometer. Map contouring for all figures was done both by hand and by computer using the Calcomp plotter. Similar results were obtained from both methods.

Results

Cell abundance is presented as though the samples were collected synoptically when collection times varied up to 2 wk,

depending on cruise tracks, weather conditions, and year sampled. The dominant organism from plankton material studied for this survey was *G. excavata*, with other dinoflagellates present to a lesser degree for each of the 5 yr. These included *Scrippsiella trochoidea, Ceratium longipes, C. minutum, C. furca, Gyrodinium aureoleum, Dinophysis* spp., and several species of large peridinians. Tintinnids observed included *Helicostomella* spp., *Favella* spp., and *Ptychocylis* spp. The ciliate *Mesodinium rubrum* was observed at many locations. Mean temperatures for the surface waters were between 11.6 and 12.6°C for the five periods observed. Salinity values ranged from 30.0 to 32.0‰. Statistical analysis of temperature, salinity, and *Gonyaulax* number data for each year resulted in no statistically significant correlations between environmental variables and *Gonyaulax* abundance for the years 1980, 1981, 1982, and 1984. Since temperature and salinity did not vary appreciably during the five summers, the differences in cell numbers from year to year must have been related to other factors.

During all 5 yr, blooms of *G. excavata* were of sufficient magnitude to cause shellfish toxin levels to rise, resulting in a ban on harvesting. However, on August 23, 1980, shellfish toxicities reached levels as high as 8200 μg saxitoxin (STX) equiv./100 g in soft-shell clams (*M. arenaria*) at Crow Harbour, New Brunswick. For all following years, clams had detectable toxicity levels during July and August but at substantially lower levels.

Distribution maps for the incidence of *G. excavata* motile cells are given in Fig. 2. The 1980 bloom was very intense, with vegetative cells observed at 84% of the 168 stations during August 14–20. Cell concentrations as high as 1.8×10^7 cells/L which caused a reddish discoloration of the water were recorded at Station 86A (Fig. 1) in the southeastern Bay of Fundy. The greatest concentrations of *G. excavata* were found in the southeastern Bay of Fundy along the coast of Nova Scotia (Fig. 2). High concentrations in 1980 extended offshore to areas east and north of Grand Manan Island where highest concentrations of *G. excavata* cysts were observed during the winter of 1980–81 (White and Lewis 1982).

Gonyaulax excavata cells were observed at 41% of the 122 locations sampled during the summer of 1981 (Fig. 2). Total numbers of cells were low to nonexistent throughout the sampling area, with 1.06×10^3 cells/L at Station 58 being the highest concentration found. From these results, one might initially assume that sampling occurred during a nonbloom period. However, routine weekly monitoring of a station north of Grand Manan, Prince 5 (44°57′N, 66°51′W), was carried out between May and October of that year, indicating that the highest levels for 1981 were obtained during the week beginning July 13 with a concentration of 1.4×10^3 cells/L, and shellfish toxicity levels at Crow Harbour increased to 910 on August 10. The geographic sampling during 1981 was July 31 – August 10. Due to the low counts from the 1981 samplings, no fusing gametes or new hypnozygotes (cysts) were observed. Twenty duplets were found at Station 61, and 20 duplets were found at Station 129 (Fig. 1).

Results from the 1982 sampling showed 91% of the locations sampled to have *G. excavata* cells present. The sampling area for 1982 was reduced to 85 stations from the previous years to exclude the outer approaches to the Bay of Fundy and a portion of the inner Bay (Fig. 2). Normal vegetative cells dividing asexually (duplets) were more prevalent for this sampling period (Fig. 3) than sexually fusing gametes (Fig. 7) which were observed at lower densities over much of the region. This high occurrence of duplets in asexual division indicates that sampling occurred in the early stages of bloom development. *Gonyaulax excavata* concentrations for this 1982 survey were at a maximum of 8.78×10^4 cells/L at Station 60.

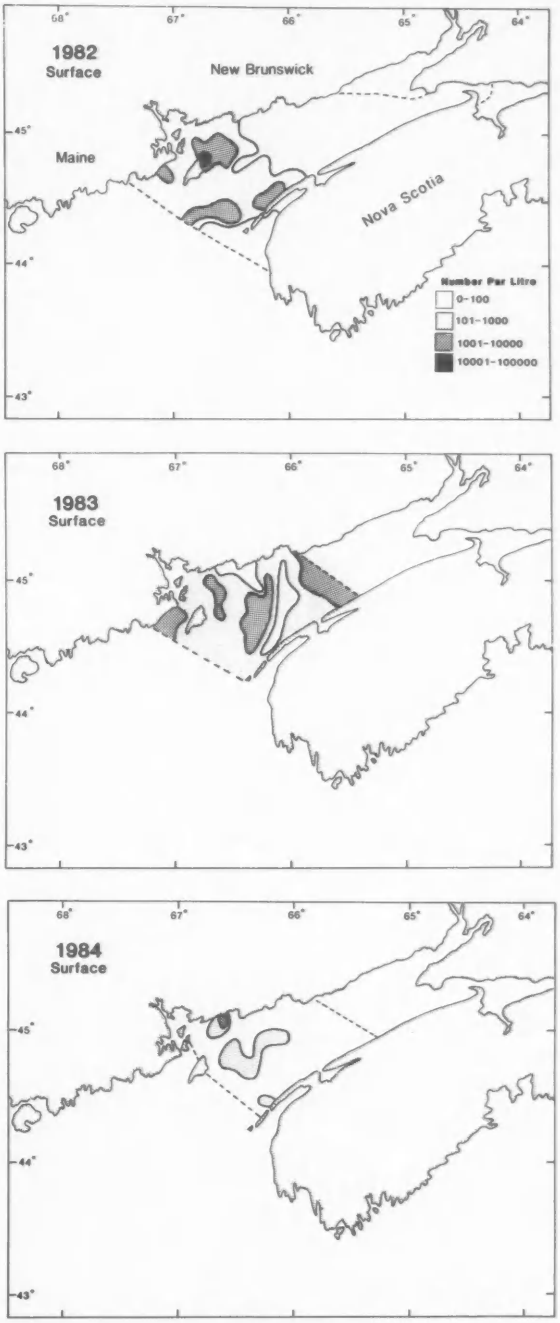


FIG. 3. Surface distribution and abundance of *G. excavata* asexually dividing cells (duplets).

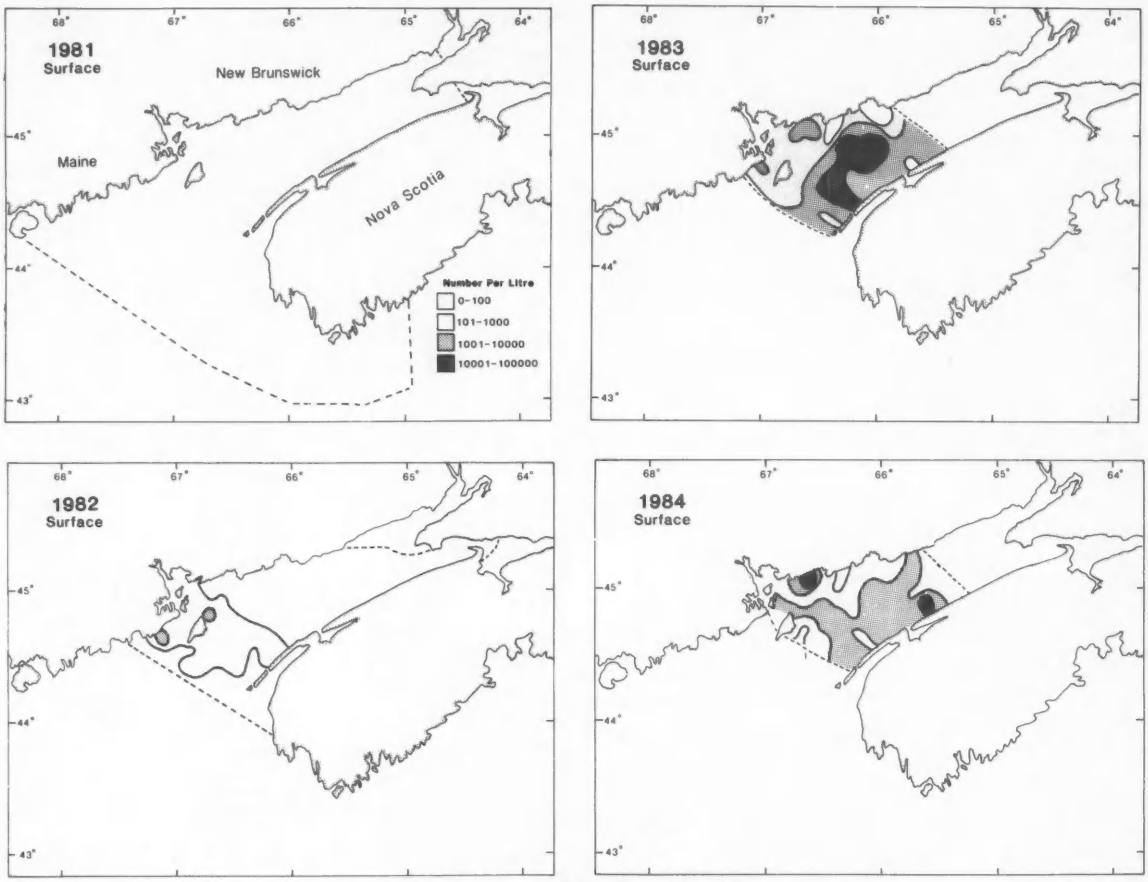


FIG. 4. Planozygote distribution at the surface.

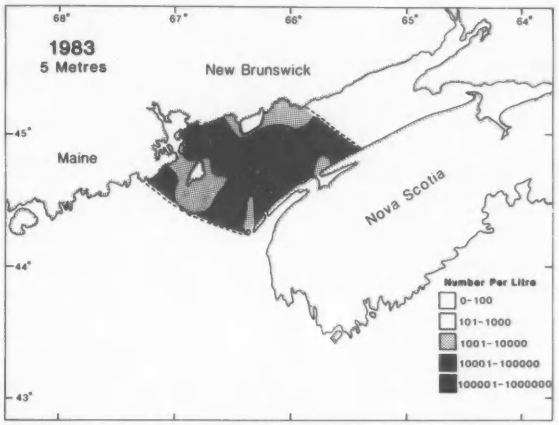
Gonyaulax excavata motile cells were observed at all locations sampled both at the surface and at a depth of 5 m during 1983 and 1984 (Fig. 2, 5). The distributions for the surface and 5 m were similar for both years, with slightly higher concentrations observed in the surface samples. Highest concentrations in 1983 were 1.56×10^5 cells/L at Station 71. The greatest numbers of motile cells for 1984 were at Station 56 with 2.16×10^5 cells/L. Distribution and abundance for planozygotes for these 2 yr at both the surface and at 5 m are shown in Fig. 4 and 6. Ninety-four percent of all stations had planozygotes observed in 1983 and 97% in 1984. Sampling for 1983 seems to have occurred earlier during the bloom than 1984, since duplets were observed in 89% of the 1983 samples as opposed to 23% for the latter (Fig. 3).

No hypnozygotes were observed during the 1981 or 1983 samplings. Forty newly formed cysts per litre were observed at Station 111 during 1982. Surface samples from nine locations (Stations 53, 60, 61, 84, 88, 90, 91, 98, 109) in 1984 had 20–40 cysts/L except Station 90 where 2.56×10^3 cysts/L were found. At the 5-m depth for the same year, cysts were observed at Stations 87 and 89 in concentrations of 20 and 60 cysts/L, respectively.

Discussion

The high concentration of *G. excavata* cells found in the central Bay of Fundy (east of Grand Manan Island to Digby, Nova Scotia, and to Saint John, New Brunswick) is consistent with the direction of the currents and water patterns within the Bay of Fundy. Inflow from the Gulf of Maine eddy (located south of the Bay of Fundy to the east of Maine and southwest of Nova Scotia) occurs along the southern entrance to the Bay close to the coast of Nova Scotia (Bumpus 1960; Bumpus and Lauzier 1965). Much of this inflow crosses over to the north side of the Bay at an area northeast of Digby, Nova Scotia, to the Saint John area of New Brunswick (Godin 1968; Iles 1975; Greenberg 1984). The outflowing waters tend to run south and west along the New Brunswick coast to round Grand Manan Island to the east in a clockwise direction and flow either along the coast of Maine or cross the Bay and flow along the coast of Nova Scotia (Hachey and Bailey 1952). A cyclonic circulation of the surface and bottom waters occurs in the southwestern region of the Bay of Fundy east of Grand Manan. Tidal currents of 100 cm/s or greater from the region give rise to tremendous mixing throughout the waters, with tidal ranges of 8 m at the mouth of the Bay and 16 m at the head (Greenberg 1983; Daborn 1986).

During the 5-yr survey, the majority of *G. excavata* motile cells were observed between the mouth of the Bay of Fundy and an area between Saint John, New Brunswick, and northeast of Digby, Nova Scotia, which follows the current patterns deter-



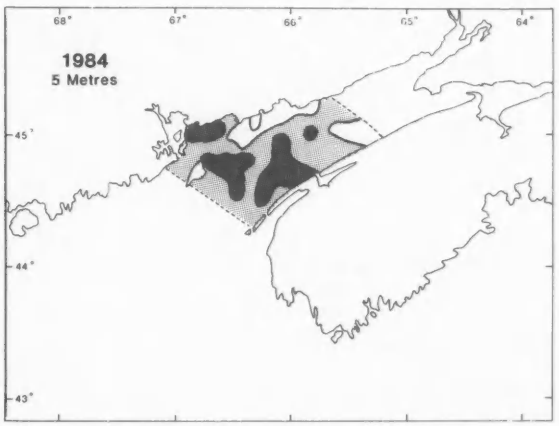
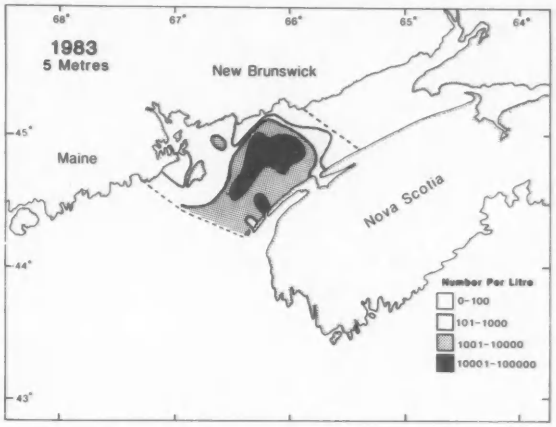


FIG. 5. Concentrations of *G. excavata* at a depth of 5 m.



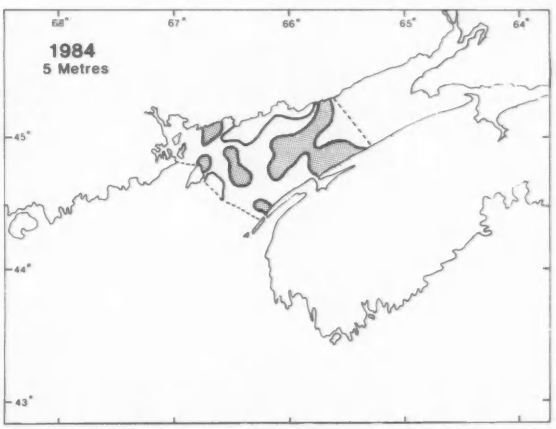


FIG. 6. Distribution and abundance of planozygotes at a depth of 5 m.

mined for the Bay of Fundy (Godin 1968). The findings of low numbers of cells were consistent for the inner portions and basins at the head of the Bay (Fig. 2) where residual current patterns are not as prevalent as in the remainder of the Bay (Godin and Gutiérrez 1986).

The surface and bottom circulations in the Bay play an important role in the distribution of cysts, their distribution as they hatch into motile cells, and the retention of the cells within the system year after year. Cyst surveys of the Bay of Fundy during the winters of 1980–83 revealed moderate to low numbers of resting cysts occurring throughout most of the Bay and inshore, with rich deposits found offshore east and north of Grand Manan Island (White and Lewis 1982; J. L. Martin, unpubl. data). The fine silt/clay (LaHave clay) characteristic to this area is a result of active sediment deposition caused by relatively low tidal current velocities from the counterclockwise gyre of both surface and bottom water (Fader et al. 1977). Cysts are deposited to the area in a similar manner. The LaHave clay provides an ideal resting location as opposed to the Sambro sand (a net erosional sediment) along Nova Scotia and the glacial till in the central Bay (Fader et al. 1977) where few or no cysts were found during benthic surveys conducted during the winters of 1980–83. Highest concentrations of *G. excavata* motile cells were also located in the areas east and north of Grand Manan Island, suggesting that this area serves as a major source for initiating summer blooms.

During August 1980, high concentrations of *G. excavata* cells causing red patches in the water were located in the southeastern region at Station 86A (Fig. 1, 2). This occurrence may be attributed to the circulation processes gathering hatching cysts from the LaHave clay beds and dispersing them to this particular area in the Bay. It has been established that water discolourations or high concentrations of dinoflagellates occur most often on hydrographic fronts or due to the convergent circulation systems induced about the fronts, and this could play a role in initiating dinoflagellate growth (Seliger et al. 1981). Pingree et al. (1975) discussed frontal regions as areas with combinations of high nutrients and a shallow upper mixed layer creating conditions suitable for rapid growth of phytoplankton. The three major frontal convergences within the Bay of Fundy are north of Grand Manan Island; south of Saint John Harbour, New Brunswick; and northwest of Digby, Nova Scotia, extending toward Saint John (Greenberg 1984; Loder and Greenberg 1986). However, frontal convergences, the local accumulations, and their effects alone cannot explain the wide distribution and patchiness of the *G. excavata* cells found during this sampling during five bloom periods. There is evidence for the years 1980, 1982, 1983, and 1984 of high concentrations of *G. excavata* motile cells located great distances from the deter-

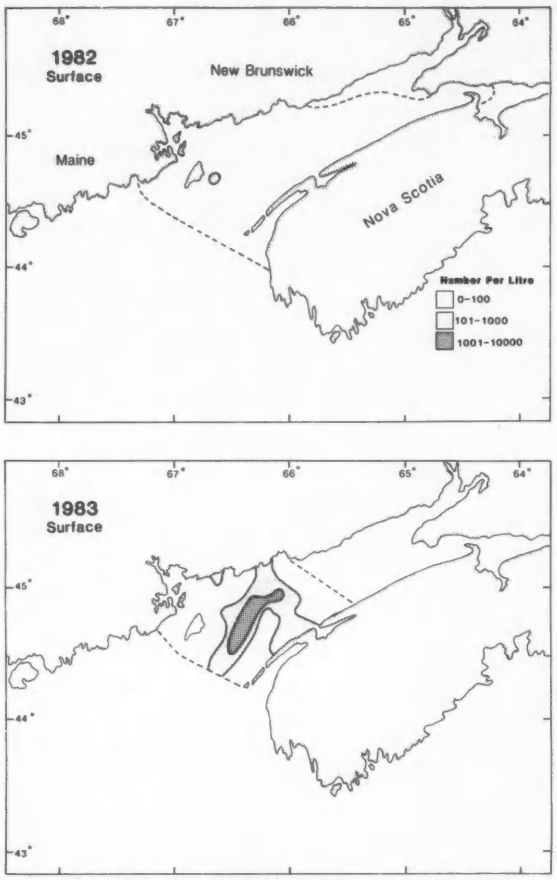


FIG. 7. Distribution and abundance of fusing cells at the surface.

mined frontal boundaries. A combination of winds, tidal mixing, frontal movements, and other physical effects that include a vertical transfer of water masses must play an important role in the dispersion of cells and nutrients. A significant correlation exists between shellfish toxicity and the 18.6-yr cycle of lunar modulation with the tides, indicating periods of intense toxicity in the mid-1940's, early 1960's, and late 1970's (White 1987).

Anderson et al. (1983) observed similar annual variations in abundance to those of the Bay of Fundy for 1980 and 1981 along the northeast coast of the United States. Similarly, *G. excavata* cells were present in high concentrations during 1980, with large numbers of new cysts deposited in surface sediments followed by a 1981 bloom period with a low percentage of the encysted population hatching, resulting in an almost nonexistent bloom period. We assume that many cysts deposited are dormant from year to year without germination because the 1982, 1983, and 1984 bloom periods were considerably more productive than 1981.

Patchiness in cell distribution and abundance may be atttibuted to some extent to experimental error. Lund et al. (1958) estimated an error of ± 10% when counting at least 400 cells. There is also a variation in cell number from two samples from the same location or in the pattern of sampling with samples taken at any phase of the tide. Vertical profiles for migration studies have proven that *G. excavata* cells in the Bay of Fundy tend to remain at the surface both day and night, permitting continuous sampling (J. L. Martin, unpubl. data). In drawing the contours, there is an element of error where generalizations are made that all sampling locations within a designated contour actually fall into a particular category. However, the data do signify a real difference in areas with high concentrations of *G. excavata* as opposed to those with few. Although *G. excavata* was the predominant organism in samples counted, there was an additional error in distinguishing between *G. excavata* and *S. trochoidea*, as discussed by White (1986). For these counts, questionable cells were not counted as *G. excavata*, thus biasing towards an underestimation of actual cell numbers. Therefore, the contours may indicate slightly less cells than were actually present. However, samples with high numbers of *G. excavata* cells tended to have very few, if any, other organisms present. It must also be noted that sexual gametes were difficult to distinguish from vegetative cells unless they were fusing. All planozygotes were distinguished as cells greater than 43 μm.

Sampling during 1983 and 1984 carried out at both the surface and at 5 m shows very similar contouring for the surface and 5 m for each year, suggesting that the samplings for 1980, 1981, and 1982, although the surface was the sole depth of sampling, were representative of actual occurrences.

In summary, the offshore area in the southwestern Bay of Fundy seems to serve as the major source for *G. excavata* in the Bay and under ideal conditions along the northeastern coast of the United States. The high number of cells during one year resulting in numerous cysts deposited does not appear to be related to the size of the next year's bloom. Results from this survey suggest that further study is required to determine the cause of continued unacceptable shellfish toxin levels in the southern Bay of Fundy.

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Patterns in Biomass and Cover of Aquatic Macrophytes in Lakes: A Test with Florida Lakes[1]

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Data from 69 Florida lakes were used to test 15 empirical models that were developed from a worldwide data base to describe the biomass and cover of aquatic macrophytes in lakes. Ten of the models failed to provide useful predictions in Florida because the models did not adequately reflect the limnological characteristics of Florida lakes. Submerged and emergent biomass in the Florida lakes was predicted by the models that estimated these parameters from the areal cover of submerged and emergent vegetation. Total macrophyte cover in Florida lakes could be predicted from a model based on lake size, annual irradiance at the surface, and the mean annual irradiance within the mean depth of the lake. Even the best models, however, overestimated submerged plant biomass and cover in highly colored (>400 Pt–Co units) lakes and lakes with steep (slope >15%) littorals. This suggests that the influence of light (quantity and quality) and littoral slope on the abundance of aquatic macrophytes needs additional research before improved empirical models can be developed for lakes located in limited geographic regions.

Des données ayant trait à 69 lacs de Floride ont été utilisées pour tester 15 modèles empiriques élaborés à partir d'une base de données mondiale afin de décrire la biomasse et la couverture de macrophytes aquatiques des lacs. Dix des modèles ne pouvaient permettre d'obtenir des prévisions utiles car ils ne reflétaient pas adéquatement les caractères limnologiques des lacs de Floride. La biomasse immergée et émergée des lacs de Floride a pu être prévue par les modèles qui estimaient ces paramètres à partir de la superficie couverte par la végétation immergée et émergée. La couverture totale des macrophytes des lacs de Floride pouvait être prévue à l'aide d'un modèle reposant sur la taille du lac, le rayonnement annuel à la surface et le rayonnement annuel moyen à la profondeur moyenne du lac. Mais même les meilleurs modèles surestimaient la biomasse des plantes immergées et la couverture dans les lacs à eau fortement colorée (>400 unités Pt–Co) et les lacs à littoraux de forts gradients (pente >15 %). Cela porte à croire qu'il faudra réaliser des recherches plus poussées sur l'influence de la lumière (quantité et qualité) et de la pente du littoral sur l'abondance des macrophytes aquatiques avant qu'il ne soit possible d'améliorer les modèles empiriques pour les lacs situés dans des régions géographiques limitées.

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Duarte et al. (1986) developed 15 quantitative models to describe the biomass and cover of aquatic macrophytes in lakes. These models were developed using data from lakes that differed greatly in morphometry (i.e. lake area, mean depth, and maximum depth) and water transparency. The lakes were also located in vastly different geographic and climatic regions ranging from the tropics to the subarctic. The predictive ability of the models, however, has not yet been tested for an independent set of lakes located within a limited geographic location. Here, we test the ability of the models developed by Duarte et al. (1986) to predict the aquatic macrophyte biomass and cover in 69 central Florida lakes.

Methods

The macrophyte communities of 69 central Florida lakes (29°N, 81°W) were sampled once during the summer (June to September) of either 1985 (55 lakes) or 1986 (14 lakes). Using existing bathymetric maps, we randomly located 10 sampling transects around the perimeter of each lake. At each transect, we randomly established a sampling station in the submerged and emergent plant zones (20 stations per lake). The aboveground plant biomass within a 0.25-m^2 quadrat was collected at each station by divers. Sampled plants were placed in nylon mesh bags, spun to remove excess water, and weighed to the nearest 0.10 kg fresh weight. The width of the emergent zone was then directly measured with a calibrated range finder and the maximum depth of colonization by submerged plants was measured by use of a recording fathometer (Maceina and Shireman 1980). Water samples were collected from three midlake stations to measure specific conductance, color, and algal biomass as measured by chlorophyll *a* concentrations (APHA 1980). Water transparency was also measured at these stations by use of a 20-cm black and white Secchi disc. The transparency values were then used to calculate annual irradiance at the mean depth and the average irradiance within the mean depth following the procedure described in Duarte et al. (1986).

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TABLE 1. Mean and range for the limnological and macrophyte characteristics measured in Florida lakes during 1985 and 1986. Numbers in parentheses are the corresponding values from Duarte et al. (1986).

Variable	Mean	Range
Area (ha)	431 (24 270)	3.2 – 12 412 (0.04 – 2.5 × 10^6)
Maximum depth (m)	4.5 (21.8)	0.7 – 9.0 (1.0 – 310)
Mean depth (m)	2.6 (7.7)	0.3 – 5.8 (0.2 – 152)
Secchi disc (m)	2.4 (2.8)	0.2 – 6.0 (0.3 – 16.0)
Total macrophyte cover (%)	55.6 (44.1)	0.5 – 100 (0.0 – 100)
Submerged plant cover (%)	30.2 (35.0)	0.0 – 99 (0.0 – 100)
Emergent plant cover (%)	30.1 (12.3)	0.5 – 100 (0.0 – 100)
Submerged plant biomass (t dry wt·ha^{-1})	1.6 (3.1)	0.0 – 16.6 (0.02 – 24.6)
Emergent plant biomass (t dry wt·ha^{-1})	3.7 (15.1)	0.2 – 12.1 (0.1 – 120)

TABLE 2. Correlation matrix for limnological characteristics of Florida lakes. Only values with $P < 0.05$ are shown. A = surface area; Z = mean depth; Z_{max} = maximum depth; S = slope; Sd = Secchi disc; Iz = annual irradiance at the mean depth. Area (A) log-transformed prior to the computation of the correlations.

Variable	A	Z	Z_{max}	S	Sd	Iz
A	—	—	—	0.60	—	—
Z		—	0.75	−0.46	—	−0.58
Z_{max}			—	−0.30	0.54	—
S				—	−0.29	—
Sd					—	0.52

The total area colonized by submerged plants was calculated by planimetry of the area above the mean depth of maximum colonization (estimated from the fathometer transects). The total area covered by emergent macrophytes was estimated by planimetry using the average width of the area colonized by emergent plants. To compare our plant biomass values with the values used by Duarte et al. (1986), we also assumed plant water content to be 90% of fresh weight (Westlake 1965). The average biomass of the different plant groups was estimated by averaging the values obtained at each sampling station. Because submerged plants were detected in all the lakes if sufficient effort was expended to find small areas of colonization, we assumed that their biomass was equal to 10 g dry wt·m^{-2} and that their coverage was equal to 0.5% of the lake area in all lakes where submerged plant cover or biomass was below our normal detection limits.

The equations developed by Duarte et al. (1986) to predict the biomass and cover of submerged, emergent, and total macrophytes are

(1) $\ln A_s = 0.91 \ln A - 1.1$

(2) $\ln B_s = 0.89 \ln A - 1.42$

(3) $\ln A_s = 0.94 \ln A + 0.85 \ln Iz - 3.7$

(4) $\ln B_s = 0.95 \ln A + 1.12 \ln Iz - 4.6$

(5) $\ln B_s = 0.99 \ln A_s + 0.37$

(6) $R_{bs}^{0.5} = 0.06 P^{0.5} + 0.05 Iz - 5.6 \cdot 10^{-4} Iz^2 - 1.3$

(7) $\%A_s = 1.4 Iz + 0.07 L_{ic} - 24 S_{al} - 0.90$

(8) $\ln A_e = 1.0 \ln A - 2.6$

(9) $\ln A_e = 0.72 \ln A + 0.69 \ln S + 0.72$

(10) $\%A_e = 2.81 \ln A - 0.21 Iz - 6.58 \ln Z_{max}$

(11) $\ln B_e = 1.1 \ln A - 1.4$

(12) $\ln B_e = 0.57 \ln A + 1.34 \ln S + 4.77$

TABLE 3. Performance of the models developed by Duarte et al. (1986) in the prediction of submerged macrophyte biomass and cover in Florida lakes. Asterisks indicate intercept (a) and slope (b) values that are significantly different from 0 and 1, respectively. R^2 is the percent of the variance in the Florida lakes accounted for by the predicted equations and $SE_{\ln est}$ is the standard error of the predictions for the Florida lakes. Numbers in parentheses are the nominal errors for the original models as given by Duarte et al. (1986).

Y	Eq.	a	b	R^2	$SE_{\ln est}$
A_s (ha)	1	−0.2	1.1	0.28	2.05 (1.47)
B_s (t dry wt)	2	−0.07	0.83	0.11	3.29 (3.04)
A_s (ha)	3	0.08	0.45*	0.48	1.44 (1.05)
B_s (t dry wt)	4	−0.87*	1.20	0.65	2.05 (2.14)
B_s (t dry wt)	5	−0.46	1.13	0.90	0.76 (1.26)
R_{bs} (t dry wt·ha^{-1})	6	−8.6*	4.03*	0.29	0.70* (0.77)*
$\%A_s$	7	0.1	0.33*	0.37	24.7 (11.2)

*Standard error of the est$^{0.5}$.

(13) $\ln B_e = 1.17 \ln A_e + 0.89$

(14) $R_{be} = 4.93 \ln A + 0.75 \text{ lat} + 62.5 (Z/Z_{max}) - 10 \ln Z - 6$

(15) $\ln A_m = 0.97 \ln A + 0.98 \ln I_z + 0.009 L_{ic} - \ln I_a$

where A is the lake area in hectares, I_a, Iz, and I_z are the annual irradiance at the surface, at the mean depth, and the average irradiance within the mean depth, respectively, in kilocalories per square centimetre per year, P is the mean annual precipitation in millimetres per year, L_{ic} is the length of ice cover in days, S is the steepness of the lake basin ($A^{0.5}/Z$), Z is the lake's mean depth in metres, Z_{max} is the lake's maximum depth in metres, lat is the latitude, A_s, A_e, and A_m are the total area covered by submerged, emergent, and total macrophytes in hectares, B_s and B_e are the total submerged and emergent biomass in metric tons dry weight, R_{bs} and R_{be} are their biomass per unit area colonized in metric tons dry weight per hectare, and $\%A_s$ and $\%A_e$ are the percent lake surface area covered by submerged and emergent macrophytes. $S_{al} = 0$ when the lake has a conductivity below 1000 μS·cm^{-1} at 25°C and 1 when conductivity exceeds 1000 μS·cm^{-1}. Note that Eq. 6 and 15 differ from those published in Duarte et al. (1986) because the original equations were published with errors. The correct equations are, therefore, given here.

The predictive ability of the models was assessed by using linear regression analysis to compare the predicted cover and biomass of the different plant groups with the values measured

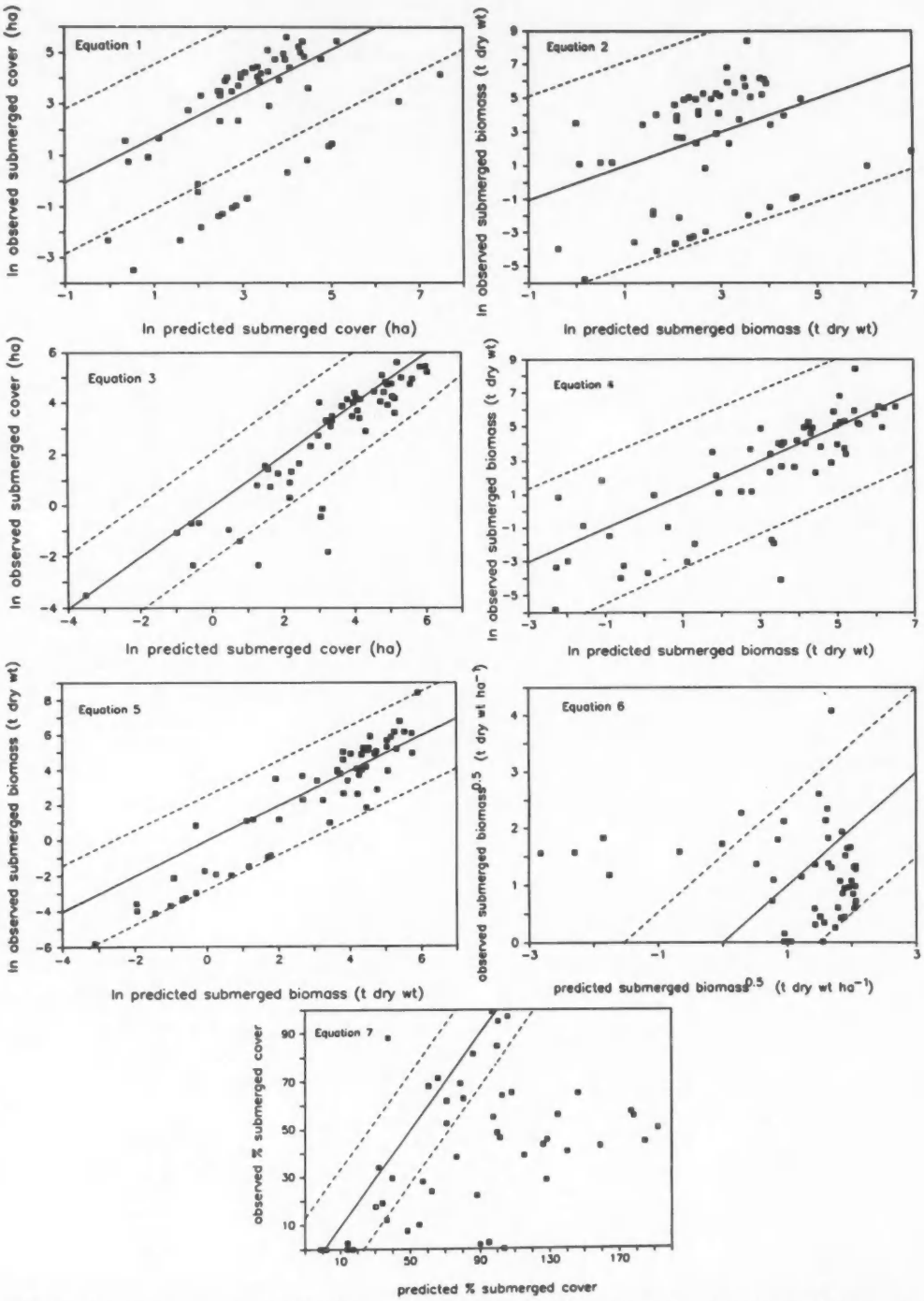
Equation 1
ln observed submerged cover (ha)
ln predicted submerged cover (ha)
Equation 2
ln observed submerged biomass (t dry wt)
ln predicted submerged biomass (t dry wt)
Equation 3
ln observed submerged cover (ha)
ln predicted submerged cover (ha)
Equation 4
ln observed submerged biomass (t dry wt)
ln predicted submerged biomass (t dry wt)
Equation 5
ln observed submerged biomass (t dry wt)
ln predicted submerged biomass (t dry wt)
Equation 6
observed submerged biomass$^{0.5}$ (t dry wt ha^{-1})$^{0.5}$
predicted submerged biomass$^{0.5}$ (t dry wt ha^{-1})
Equation 7
observed % submerged cover
predicted % submerged cover

FIG. 1. Relationships between submerged macrophyte biomass and cover in Florida lakes and predictions from the empirical regression equations (Eq. 1–7) developed by Duarte et al. (1986). Solid line is the 1:1 line between observed and predicted values and the broken lines represent the 95% confidence limits established by Duarte et al. (1986) for each empirical equation.

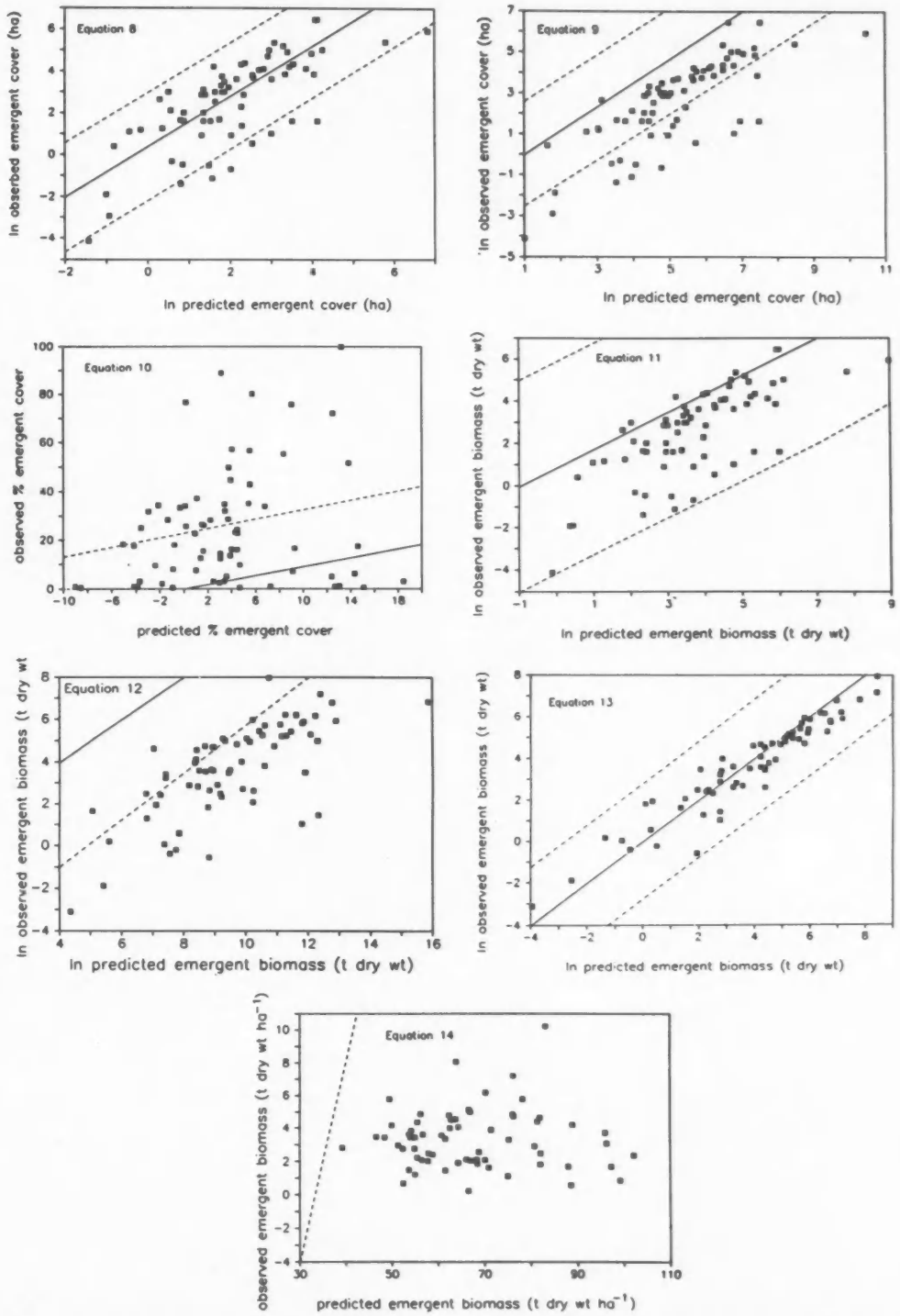
Equation 8
ln observed emergent cover (ha)
ln predicted emergent cover (ha)
Equation 9
ln observed emergent cover (ha)
ln predicted emergent cover (ha)
Equation 10
observed % emergent cover
predicted % emergent cover
Equation 11
ln observed emergent biomass (t dry wt)
ln predicted emergent biomass (t dry wt)
Equation 12
ln observed emergent biomass (t dry wt)
ln predicted emergent biomass (t dry wt)
Equation 13
ln observed emergent biomass (t dry wt)
ln predicted emergent biomass (t dry wt)
Equation 14
observed emergent biomass (t dry wt ha^{-1})
predicted emergent biomass (t dry wt ha^{-1})

FIG. 2. Relationships between emergent macrophyte biomass and cover in Florida lakes and predictions from the empirical regression equations (Eq. 8–14) developed by Duarte et al. (1986). Solid line is the 1:1 line between observed and predicted values and the broken lines represent the 95% confidence limits established by Duarte et al. (1986) for each empirical equation.

TABLE 4. Performance of the models developed by Duarte et al. (1986) in the prediction of emergent macrophyte biomass and cover and the total macrophyte cover (A_m) in Florida lakes. Asterisks indicate intercept (a) and slope (b) values that are significantly different from 0 and 1, respectively. R^2 is the percent of the variance in the Florida lakes accounted for by the predicted equations and $SE_{\ln est}$ is the standard error of the predictions for the Florida lakes. Numbers in parentheses are the nominal errors for the original models as given by Duarte et al. (1986).

Y	Eq.	a	b	R^2	$SE_{\ln est}$
A_e (ha)	8	−0.17	1.06	0.54	1.48 (1.33)
A_e (ha)	9	−2.43	1.10	0.60	1.38 (1.28)
$\%A_e$	10	20.76*	0.40*	0.18	21.6 (11.6)
B_e (t dry wt)	11	−0.21	0.99	0.49	1.59 (2.53)
B_e (t dry wt)	12	−5.31*	1.03	0.51	1.55 (2.47)
B_e (t dry wt)	13	−0.42	0.97	0.90	0.69 (1.45)
R_{he} (t dry wt·ha^{-1})	14	2.76*	0*	0.04	58[a] (17)[a]
A_m (ha)	15	−0.39	1.08	0.73	1.02 (0.86)

[a]Standard error of the untransformed estimate.

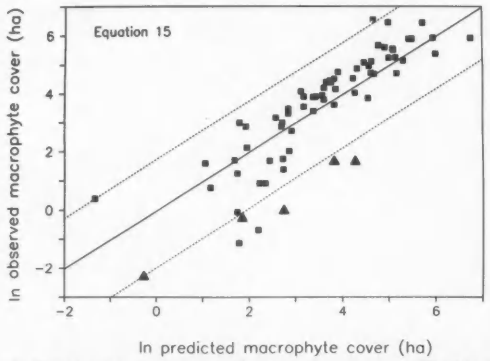

FIG. 3. Relationship between total macrophyte cover in Florida lakes and predictions from the empirical regression equation (Eq. 15) developed by Duarte et al. (1986). Solid line is the 1:1 line between observed and predicted values and the broken lines represent the 95% confidence limits established by Duarte et al. (1986) for Eq. 15. Triangles represent lakes stocked with grass carp to control aquatic macrophytes.

in the lakes. To determine the precision of the predictions, the standard error of estimates for these equations were compared with the nominal errors of the models reported in tables 3 and 4 by Duarte et al. (1986). Because the ranges of limnological variables in Florida lakes were smaller than those in the data set used to develop the models, it is possible that the models could be precise (i.e. the observations lie within the 95% confidence limits of the models) without significantly explaining variance in macrophyte biomass and cover of the Florida lakes. We therefore calculated the coefficient of determination (R^2) between the predicted and observed values. The existence of bias in the predictions was assessed by testing the hypotheses (t-test) that the intercept of the regression equation for predicted and observed values did not differ from 0 and that the slope did not differ from 1. We also produced scatterplots to illustrate relationships between our observed measures of plant abundance, the 1:1 line for observed and predicted values, and the 95% confidence limits for the predictive equations developed by Duarte et al. (1986).[2]

[2]Data used in these analyses are available, at a nominal cost, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

Results and Discussion

Lake Characteristics

The Florida lakes sampled during this study were formed by karst processes (Sellards 1914; Cooke 1939; Stubbs 1940). Although all the lakes were solution lakes, the basins ranged from broad, shallow basins to simple or complex dolines. Some lakes had a deep sinkhole along the margin of the lake. In these lake types, most areas were shallow, but the lakes still had a deep maximum depth. Basin morphometries were, therefore, not adequately described by morphometric indices developed for northern lakes (i.e. Hakanson 1981; Carpenter 1983). The broad shallow lakes (Nicatoon, Halfmoon, Big Bass, Bunch Ground Pond, and Penner Pond) supported close to 100% cover of emergent and floating-leaved vegetation and were more similar to marshes than lakes. Five of our study lakes (Baldwin, Clear, Pearl, Susannah, and Wales) were stocked with grass carp (*Ctenopharyngodon idella*) or hybrid grass carp in the 1970's for the control of submerged macrophytes. Macrophyte communities were, therefore, severely reduced from their natural status (Leslie et al. 1983; Shireman et al. 1985).

The limnological and macrophyte characteristics of the Florida lakes differed from those of the lakes used by Duarte et al. (1986) to develop their models (Table 1). Lake surface areas for the Florida lakes ranged from 3.2 to 12 412 ha (average 431 ha) compared with 0.04 ha to 2.5 × 10^6 ha (average 24 270 ha; published in error as 194 ha in original paper) in the data set used by Duarte et al. (1986). The Florida lakes were also much shallower in terms of mean depth and maximum depth (Table 1). Water transparency (Secchi disc values) in the Florida lakes ranged from 0.2 to 6.0 m compared with Duarte et al.'s (1986) range of 0.3–16 m. Unlike the lakes in the data set used by Duarte et al. (1986), the Florida lakes did not become deeper and clearer as lake size increased (Table 2). Irradiance at the mean depth of the Florida lakes was also not correlated with variables (length of the ice-free season and incoming irradiance) influenced by latitude as in the data set used by Duarte et al. (1986). Instead, underwater irradiance was correlated with water transparency and lake mean depth (Table 2). The percent lake area covered by submerged ($\%A_s$), emergent ($\%A_e$), and total ($\%A_m$) macrophytes in the Florida lakes was similar to the values reported by Duarte et al. (1986), but the ranges in the biomass of submerged and emergent plants per unit area colonized were smaller (Table 1). The average cover of emergent vegetation was also over twofold greater and the range of emergent biomass 10-fold smaller in the Florida lakes (Table 1).

Submerged Macrophyte Models

Our initial attempts to test the submerged macrophyte models of Duarte et al. (1986) were frustrated because 11 lakes were statistical outliers for all analyses. Ten of the lakes had lower submerged macrophyte abundances than expected. Five of these lakes were the broad, shallow, marsh-like lakes that had close to 100% cover of emergent and floating-leaved vegetation, which greatly limited habitat available for submerged macrophyte growth. The other five lakes were lakes purposely stocked with grass carp to remove submerged vegetation. Highly colored (>400 Pt–Co units) Lake Eaton, however, supported a much greater biomass and cover of submerged plants than expected. This lake was covered by a free-floating submerged macrophyte (*Ceratophyllum demersum*), which did not grow

from the bottom and was therefore not influenced by underwater irradiance to the same extent as rooted submerged macrophytes. Because none of these conditions were present in the original data set used by Duarte et al. (1986), we removed these lakes from our data set prior to testing the submerged macrophyte models.

Submerged macrophyte cover (A_s) and biomass (B_s) values predicted from the equations based solely on lake surface area (Eq. 1 and 2, respectively) were significantly, but weakly related ($R^2 = 0.28$ for A_s; $R^2 = 0.11$ for B_s) to the measured values in the Florida lakes (Fig. 1; Table 3). The prediction errors for the Florida lakes were also larger than the nominal errors reported by Duarte et al. (1986) for Eq. 1 and 2 (Table 3). The weak relationships between lake area and A_s and B_s, however, resulted primarily because a number of the lakes had reduced submerged macrophyte communities due to limited water transparency. Water transparency was reduced primarily by high concentrations of organic color (>200 Pt–Co units) or chlorophyll *a* (>50 mg·m^{-3}). We therefore suggest that these simple equations are of limited value for predicting A_s and B_s because light availability is often the major environmental factor limiting submerged macrophytes in lakes (Canfield et al. 1985; Chambers and Kalff 1985).

Equations 3 and 4 estimate submerged macrophyte cover and biomass from lake area and the irradiance at the mean depth of the lake. Both of these equations performed better ($R^2 = 0.48$ for A_s; $R^2 = 0.65$ for B_s) than Eq. 1 and 2 (Fig. 1; Table 3) for the Florida lakes, thus further supporting the importance of light availability. The prediction error for the submerged cover was larger than the nominal error associated with the original regression equation, but the prediction error for biomass was smaller (Eq. 3 and 4, Table 3). We believe that these equations will provide useful predictions for most types of lakes, but both equations significantly overestimated (values exceeding the 95% confidence limit) the macrophyte cover and biomass of some highly colored lakes (>400 Pt–Co units) and lakes with very steep (>15%) slopes (Fig. 1). Secchi disc values for the highly colored lakes indicated that sufficient irradiance should have been available to support more extensive submerged plant communities (Canfield et al. 1985). The total irradiance reaching the bottom, therefore, may not be as important as the quality (spectral characteristics) of light reaching the bottom. Until the importance of basin slope and the quality of underwater irradiance can be determined, Eq. 3 and 4 should be used cautiously for lakes with steep littorals and highly colored lakes.

The best predictions of submerged macrophyte biomass were obtained using Eq. 5 ($R^2 = 0.90$) which estimates biomass from the total area colonized by submerged vegetation (Fig. 1). The prediction error for Eq. 5 was also smaller than the nominal error associated with the original regression equation (Table 3). The measured biomass values for two lakes with very steep littorals (slope >15%), however, were overestimated (beyond the 95% confidence limits) by Eq. 5 (Fig. 1); thus this equation may be of limited value if the slope of the littoral exceeds 15%.

Two equations (Eq. 6 and 7) proposed by Duarte et al. (1986) failed for the Florida lakes (Fig. 1). Although our measured values for the submerged macrophyte biomass per unit area colonized (R_{bs}) and the percent lake area covered by submerged macrophytes in Florida lakes ($\%A_s$) were significantly correlated ($R^2 = 0.29$ for R_{bs}; $R^2 = 0.37$ for $\%A_s$) with their respective predicted values, Eq. 6 underestimated the measured values of R_{bs} and Eq. 7 overestimated the measured values of $\%A_s$ (Table 3; Fig. 1). More than 50% of the values predicted from Eq. 7 were also beyond the 95% confidence limits established for Eq. 7. The results from our test of Eq. 6 further indicate that annual precipitation has little influence on submerged macrophytes and that Eq. 6 may be an artifact of the data set used by Duarte et al. (1986). Equation 6 was developed using data from only 39 lakes and the coefficient of determination (R^2) for Eq. 6 was 0.51, the lowest obtained by Duarte et al. (1986). We therefore conclude that Eq. 6 and 7 cannot be used to predict R_{bs} and $\%A_s$ in Florida lakes.

Emergent Macrophyte Models

Emergent cover (A_e) and biomass (B_e) values predicted from the equations (Eq. 8 and 11) based on lake surface area were significantly correlated ($R^2 = 0.54$ for A_e; $R^2 = 0.49$ for B_e) with the values measured in all 69 central Florida lakes (Fig. 2; Table 4). Ten lakes, however, had lower (i.e. beyond the 95% confidence limits) emergent abundances than expected from Eq. 8, and there was a noticeable tendency for Eq. 11 to overestimate measured values (Fig. 2). Incorporating a measure for the steepness of the lake basin (S) into the models (Eq. 9 and 12) slightly improved the correlation between predicted and measured values for A_e ($R^2 = 0.60$) and B_e ($R^2 = 0.51$), but both equations still provided biased estimates of emergent cover and biomass in the lakes (Table 4; Fig. 2). A large (>25%) number of predicted values were also beyond the 95% confidence limits established for Eq. 9 and 12 by Duarte et al. (1986). The reason for the poor performance of these equations is unclear at this time, but a source of bias in the models predicting emergent biomass may be the 10-fold lower average areal emergent biomass (Table 1) measured in the Florida lakes compared with those reported by Duarte et al. (1986). Until the sources of bias in the predictions are identified, Eq. 8, 9, 11, and 12 as formulated are of little value for predicting emergent macrophyte abundance in Florida lakes.

The predicted percent area ($\%A_e$) and the biomass per unit area (R_{be}) colonized by emergent macrophytes (Eq. 10 and 14, respectively) were poorly correlated ($R^2 = 0.18$ for $\%A_e$; $R^2 = 0.04$ for R_{be}) with the values measured in the Florida lakes (Fig. 2). Both equations provided biased cover and biomass estimates for emergent plants and most observations were beyond the 95% confidence limits established for the equations by Duarte et al. (1986). These equations are, therefore, useless in Florida and may not perform well in other geographic regions, but need to be tested. Precise and unbiased predictions of emergent biomass, however, were obtained from Eq. 13, which estimates B_e from the total area colonized by emergent plants (Table 4; Fig. 1). The prediction error was also much smaller than the nominal error given by Duarte et al. (1986) for the equation (Table 4).

Total Macrophyte Model

Values of total macrophyte cover predicted from Eq. 15 were significantly correlated ($R^2 = 0.73$) with the values measured in all 69 Florida lakes. The predictions were not biased (Fig. 3; Table 4), but the prediction error was larger than that associated with the original equation (Table 4). The prediction error, however, was larger because the model overestimated total macrophyte cover for lakes where grass carp were present, there were high concentrations of humic substances (color >400 Pt–Co units), or there were very steep (slope >15%) littorals, that prevented the development of submerged vegetation. Although we believe that Eq. 15 should be used cautiously for highly

colored lakes and lakes with steep basins, it identified lakes (beyond the 95% confidence limits) where control measures (i.e. lakes stocked with grass carp) prevented the development of submerged macrophyte communities (Fig. 3). Equation 15, therefore, might prove useful in identifying lakes where the macrophyte communities have not developed properly due to control measures.

Conclusions

Many of the models (Eq. 1, 2, 6, 7, 8, 9, 10, 11, 12, and 14) developed by Duarte et al. (1986) failed to provide useful estimates of the cover and biomass of emergent and submerged macrophytes in the Florida lakes. The relative weakness of these models may be partially explained because variability in macrophyte abundance in the Florida lakes must reflect the variability in their limnological conditions (e.g. lake morphometry, chemistry, and water transparency) rather than climatic differences (i.e. latitude, length of ice cover, and surface irradiance) among lakes, which contributed significantly to the models developed by Duarte et al. (1986). Some of these models also demonstrated weak predictive power in the original analyses (i.e. Eq. 6, 10, and 14). Their failure to predict the macrophyte abundance of our Florida lakes suggests that they may have been influenced by peculiarities in the data set used to develop them. It should be noted, however, that none of the failed models were cross-validated by Duarte et al. (1986), who developed them primarily to suggest possible patterns in the cover and biomass of aquatic macrophytes in lakes.

Five of the models (Eq. 3, 4, 5, 13, and 15) presented by Duarte et al. (1986) provided reasonable predictions of macrophyte abundance in the Florida lakes. With the exception of Eq. 4, the equations had been previously cross-validated by Duarte et al. (1986). Our tests, therefore, confirm the generality of these models and demonstrate their applicability to lakes located within a limited geographic area. Our analyses, however, suggest that the models should be applied cautiously for submerged macrophytes in highly colored lakes, lakes with very steep littorals, and lakes dominated by emergent and floating-leaved vegetation. Additional studies on the influence of color and littoral slope on the abundance of submerged macrophytes are needed to determine if inclusion of these parameters in multivariate models will improve our predictive capabilities. The models developed by Duarte et al. (1986) also ignore free-floating macrophytes (i.e. *Ceratophyllum demersum, Eichhornia crassipes*, and *Pistia stratioties*) and floating-leaved macrophytes which contribute significantly to the macrophyte communities in many lakes. Quantitative descriptions of patterns in cover and biomass for these plant types, such as those recently proposed by Smith and Wallsten (1986), may enhance our ability to predict not only total macrophyte abundance in lakes, but lakes that have the potential for aquatic weed problems.

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What is a Safe Level of Polycyclic Aromatic Hydrocarbons for Fish: Subchronic Toxicity Study on Winter Flounder (*Pseudopleuronectes americanus*)

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Dose–response relationships were evaluated for a variety of biological and biochemical indices in a subchronic toxicity study with winter flounder (*Pseudopleuronectes americanus*) exposed to sediments contaminated with a petroleum source of polycyclic aromatic hydrocarbons (PAH). Indices investigated were biologically meaningful and included muscle and liver levels of energy reserves, organ weight – body weight relationships, and general condition indices. Results support the hypothesis that many point sources of sediment hydrocarbon contamination worldwide could be harmful to fish health. Biochemical effects such as change in mixed-function oxygenase (MFO) enzyme levels and fat content of liver were altered at very low hydrocarbon levels (~1.0 μg/g), levels that we reason will likely be found in sediments over much wider geographical areas than polluted harbors, or oil development and sewage outfall sites. We hypothesized that hydrocarbons in both coastal waters and food species may often occur in sufficient concentrations to affect biological responses in fish. The fact that very low levels of hydrocarbons in sediments, water, or foods may produce biological responses in fish attests to the importance of developing criteria for assessing the toxicological significance of sublethal effects or otherwise defining genuine harmful effects in contrast with effects per se.

Les auteurs ont évalué les relations dose–réponse pour divers facteurs biologiques et biochimiques au cours d'une étude de toxicité sous-chronique portant sur des plies rouges (*Pseudopleuronectes americanus*) exposées à des sédiments contaminés par un produit pétrolier contenant des hydrocarbures aromatiques polycycliques. Les paramètres étudiés étaient significatifs du point de vue biologique et comprenaient les niveaux en réserves énergétiques des muscles et du foie, le rapport organe – poids corporel et des indices de l'état général. Les résultats appuient l'hypothèse voulant que l'existence, au niveau mondial, d'un grand nombre de sources ponctuelles de contamination des sédiments par les hydrocarbures sont nuisible aux poissons. Certains effets biochimiques, telles des modifications des teneurs en enzyme oxygénase à fonction mixte et de la teneur en lipides du foie apparaissent à des teneurs très faibles en hydrocarbures (~ 1,0 μg/g) qui, selon les auteurs, devraient exister dans des sédiments de zones géographiques beaucoup plus étendues que celles des ports pollués ou des zones de mise en valeur pétrolière ou de rejets d'eaux résiduaires. Les auteurs formulent l'hypothèse que les hydrocarbures présents dans les eaux côtières et les espèces servant de nourriture peuvent souvent y être présents en concentrations suffisantes pour modifier les réactions biologiques des poissons. Le fait que de très faibles concentrations d'hydrocarbures dans les sédiments, l'eau ou les aliments peuvent provoquer des réactions biologiques chez les poissons atteste l'importance d'élaborer des critères permettant d'évaluer la significance toxicologique des effets sublétaux ou de déterminer les effets nuisibles réels en fonction des effets notés.

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One of the most challenging problems in aquatic toxicology is evaluating the biological significance, if any, of long-term exposure to low levels of pollutants. Sediments are of particular importance because they act as sinks for a variety of biologically refractory pollutants. However, even relatively high levels of contamination may be of little biological significance if bioavailability is limited. Polycyclic aromatic hydrocarbons (PAH) (and their alkyl homologs) from petroleum and combustion sources are distributed in sediments throughout the world and have generated considerable attention because of their potential mutagenic/carcinogenic and otherwise cytotoxic properties. Both laboratory and field studies have demonstrated effects in fish exposed to waters or sediments contaminated with relatively high levels of hydrocarbons (Payne

et al. 1978; McCain et al. 1978; Engelhardt et al. 1981; Lopez et al. 1981; Fletcher et al. 1982; Haensly et al. 1982; Khan and Kiceniuk 1984; Rice 1985) and there is a critical need to establish at what level of contamination deleterious effects can be anticipated. PAH have also been specifically implicated in some environmental carcinogenesis problems in fish (Baumann et al. 1982; Black 1983; Malins et al. 1985). We have investigated dose–response relationships for a variety of indices in winter flounder (*Pseudopleuronectes americanus*) chronically exposed to sediments contaminated with different levels of petroleum hydrocarbons. The results are of importance for addressing specific questions such as (a) potential effects on fish at sites of hydrocarbon development in the offshore, (b) recovery rates of sediments contaminated by major oil spills, and (c) the high level of concern about PAH contamination in coastal and inland waters, a worldwide phenomenon.

Methods and Materials

Male winter flounder were exposed for approximately 4 mo to sediments contaminated with a range of Venezuelan crude oil concentrations. Preliminary experiments were carried out during the autumn and winter of year 1 and these were followed in year 2 with the more comprehensive study reported here. The amounts of oil mixed into 45-kg portions of dry sand were as follows: 0 (E0), 5 mL (E1), 25 mL (E2), 50 mL (E3), 250 mL (E4), and 500 mL (E5). Due to the small volumes of petroleum used, the low-level exposures had to be prepared by thoroughly contaminating a small quantity of sand and progressively contaminating larger quantities (essentially resulting in a sprinkling throughout). Sand was added to aquaria (300 L) to give a bottom layer approximately 5 cm deep and the aquaria were supplied with air and running seawater (4–5 L/min) at seasonally ambient conditions of temperature and photoperiod (Fletcher 1977). Prior to addition of flounder to the aquaria, sand (control and hydrocarbon contaminated) was mixed into the water column 2–3 times/d in order to remove any unadsorbed oil. Fish were placed in the aquaria after a further equilibration period of 7 d. The experiment was initiated on February 16, 1984, and terminated on June 18, 1984. At the termination of the exposure period, fish were killed by a blow to the head and tissues were frozen in liquid nitrogen and stored at −80°C. Winter flounder found in Newfoundland waters do not eat during the winter months, the principal period of feeding being from April to October (Fletcher and King 1978). The winter nonfeeding period was especially chosen to avoid the possibility of feeding interactions (such as a decrease in food intake) confounding the results. Also, males were chosen in preference to females because of their simpler gonadal cycle and their lower and less variable liver lipid content. In this regard it is also worth noting that in Newfoundland waters, the testes of flounder start to develop during late August and grow to a maximum weight by November (Fletcher and King 1978).

Condition factors were determined using total body weight and carcass weight (carcass weight = total weight minus the weight of gonads, liver, spleen, and digestive tract). Organ to body weight ratios were determined for the gonads, liver, spleen, kidney, and guts. The biochemical indices investigated included water, glucose, glycogen, lipid, and protein in both liver and muscle tissues and liver and kidney levels of mixed-function oxygenase (MFO) enzymes. Muscle and liver glycogen were determined using the amyloglucosidase method of Keppler and Decker (1981). Total lipids were measured gravimetrically after extraction by the method of Bligh and Dyer (1959), and proteins were determined by micro-Kjeldahl, assuming 1 mg of N to be equivalent to 6.25 mg of protein. Muscle water was determined by drying (90°C) to constant weight. The assay for MFO enzyme activity was carried out as previously described with ethoxyresorufin as substrate (Payne et al. 1985).

Effects of treatment were analyzed by one-way ANOVA and means were compared by Duncan's multiple range test. Comparisons between control and treatments at a level of significance of $P \leq 0.05$ are denoted by asterisks.

Grab samples of sediment were taken for hydrocarbon analysis at the beginning (February) and end (June) of the experiment. Hydrocarbon analysis of sediment extracts was carried out by high-pressure liquid chromatography (HPLC) with the aid of a Waters Energy Analysis Column; this gives a good approximation of the relative abundance of different classes of PAH (both parent and alkylated two- to five-ring aromatics). Ten grams of sediment was extracted with three 50-mL aliquots of methylene chloride and the pooled extracts were stored for 30 min over 10 g of anhydrous sodium sulfate to remove any excess water. The extracts were then concentated to 2.0 mL in hexane by a Kuderna–Danish apparatus and filtered through a Millex Sr 0.5-μm PTFE filter prior to analysis by HPLC. One hundred and fifty microlitres of each extract was separated on a 4.6 × 25 mm column with hexane (2 mL/min) as the mobile phase. Two-, three-, and four-ring aromatics were calculated as naphthalene, phenanthrene, fluorene, and pyrene equivalents. Components were monitored at a wavelength of 254 nm and the practical limit of detection for naphthalene, fluorene, phenanthrene, and pyrene was 30, 10, 5, and 30 ng, respectively. The recovery of petroleum hydrocarbons from sediments was approximately 95% using [^{14}C] anthracene as internal standard ($\bar{x} = 95.5 \pm 3.97$, $N = 6$ samples). The sum of the concentrations of naphthalene, fluorene, phenanthrene, and pyrene equivalents was used to estimate total concentrations of PAH in sediments (both parent and alkylated forms).

Sediments were taken from each of four tanks and analyzed separately for particle size. The four samples were uniform, with the amount retained on 1180-, 500-, 125- and 45-μm sieves being approximately 6, 17, 76, and ≤ 0.3%, respectively. This places the sediment in the fine to medium sand category with little silt. Light microscopic analysis demonstrated the particles to be worn and rounded, typical of beach weathered sand. The organic content of the sand was not determined but can be expected to be quite low, since it was essentially free of silt.

The Venezuelan crude (stored in a 4-L glass bottle in the dark) used in the study was further analyzed by both HPLC and gas chromatography – mass spectrometry (GS–MS) to determine the relationship between total levels of PAH equivalents as determined by HPLC and the actual concentrations of different classes of alkylated PAH as determined by GC–MS. In brief, the mass spectrometric analysis was carried out as follows. Oil was spiked with perdeuterated PAH standards, refluxed in methanolic KOH, and extracted with pentane. The pentane extracts were then dried over anhydrous sodium sulphate and reduced to a small volume by vacuum rotary and nitrogen jet evaporation. The extract was taken up in dichloromethane–isopropanol and applied to a precalibrated gel permeation column (Sephadex LH20) to prepare the aromatic fraction which was analyzed on a Finnigan 9500/3200 gas chromatograph – mass spectrometer. Detailed GC–MS analysis of the crude oil aromatic fraction produced a complex chro-

TABLE 1. Hydrocarbon concentrations (μg/g) in sediments.

Treatment		Naphthalene	Fluorene	Phenanthrene	Pyrene	ΣPAH
Control	Begin	ND	ND	0.004	0.045	0.049
		ND	ND	0.003	0.043	0.046
	End	ND	0.258	0.003	0.080	0.083
		ND	ND	0.004	0.053	0.057
E5	Begin	ND	ND	0.005	ND	0.005
		ND	0.775	0.009	ND	0.784
	End	ND	ND	ND	0.193	0.193
		ND	0.672	0.003	ND	0.675
E25	Begin	ND	36.275	0.119	1.460	37.854
		ND	41.619	0.130	2.105	43.854
	End	ND	13.806	0.022	ND	13.828
		ND	13.631	0.021	ND	13.652
E50	Begin	ND	54.829	0.187	2.182	57.881
		ND	56.264	0.180	ND	56.444
	End	ND	26.419	0.039	ND	26.458
		ND	35.376	0.055	ND	36.431
E250	Begin	22.626	239.486	0.749	ND	262.861
		17.247	189.330	0.594	ND	207.171
	End	ND	242.641	0.674	ND	243.315
		ND	304.309	ND	ND	304.309
E500	Begin	—	1378.621	ND	ND	1378.621
		40.900	482.453	1.583	ND	524.936
	End	18.715	208.400	0.546	ND	227.661
		18.365	205.362	0.546	ND	224.273

TABLE 2. GC–MS analysis of the PAH content (mg/g) of Venezuelan crude oil. C-0, C-1, etc., refer to degree of alkylation.

	Naphthalene	Fluorene	Dibenzothiophene	Phenanthrene/ anthracene
C-0	410	70	170	260
C-1	1 900	130	830	1100
C-2	3 800	180	1200	1000
C-3	4 400		300	470
C-4	670		120	180
Σ	11 800	380	2620	3010

matogram, and the major resolved compounds were identified by mass spectra, characteristic ions, and retention times.

Standard Reference Material consisting of a certified acetonitrile solution of several of the PAH of interest was obtained from the U.S. National Bureau of Standards (S.R.M. No. 1647). Mass spectrometer resolution and response to a fragmentation standard were required to meet USEPA criteria (Eichelberger et al. 1975).

Results and Discussion

PAH Concentrations in Sediments

The traces of PAH found in control sediments (Table 1) are likely derived from combustion sources. The Avalon region of Newfoundland is not industrialized but some level of contamination from the combustion of fossil fuels would be anticipated. Since the sediments containing the lowest levels of PAH were prepared by sprinkling small quantities of contaminated sand throughout, there was some concern about obtaining a uniform distribution of hydrocarbon contamination. However, the replicates for this type of experiment were quite satisfactory. Control and E5 sediments contained PAH levels near the practical limits of detection, so some variability would be expected. Compounds conforming to naphthalene equivalents underwent the greatest degree of "loss" or weathering and were only found at the end of the experiment in sediments contaminated with the highest level of hydrocarbons. There was also some weathering of the higher molecular weight PAH, notably in sediments containing lower levels of contamination. This is consistent with the hypothesis that weathering would be expected to be more effective in the absence of particle congealing or stickiness at lower levels of hydrocarbon contamination. In this regard it is worth noting that the concentrations of hydrocarbons in those sediments

TABLE 3. Effect of hydrocarbon-contaminated sediments on condition indices in flounder (in terms of total weight of fish). E1–E5 = treatments; condition indices are expressed as means ± SE, N = number of samples; fish condition index = T (g)/L^3 (cm) × 100 where T = total weight of fish and L = length; organ condition index = wt. organ/T × 100 where T = total weight of fish; $P^* < 0.05$ between control and treatment.

	Control	E1	E2	E3	E4	E5
Fish	1.0145 ± 0.0206 N = 24	1.0724 ± 0.0224 N = 24	1.0575 ± 0.0140 N = 22	1.0169 ± 0.0181 N = 22	1.0484 ± 0.0226 N = 19	0.9974 ± 0.0256 N = 22
Testis	6.0068 ± 0.6556 N = 23	5.9472 ± 0.6299 N = 24	6.1647 ± 0.6719 N = 22	6.8451 ± 0.6479 N = 22	7.2120 ± 0.8108 N = 19	6.4441 ± 0.6574 N = 22
Liver	0.6890 ± 0.0201 N = 23	0.7387 ± 0.0335 N = 24	0.7445 ± 0.0237* N = 22	0.8016 ± 0.0449* N = 22	1.0644 ± 0.0486* N = 19	1.1471 ± 0.0433* N = 22
Spleen	0.1565 ± 0.0136 N = 23	0.1521 ± 0.0122 N = 24	0.1679 ± 0.0119 N = 22	0.1585 ± 0.0142 N = 22	0.1147 ± 0.0127* N = 19	0.1153 ± 0.0086* N = 22
Kidney	0.3862 ± 0.0162 N = 23	0.3734 ± 0.0170 N = 24	0.3883 ± 0.0180 N = 22	0.3985 ± 0.0186 N = 22	0.3824 ± 0.0219 N = 19	0.4403 ± 0.0201 N = 22
Gut	2.7763 ± 0.1225 N = 23	2.8448 ± 0.0963 N = 24	2.8577 ± 0.1330 N = 22	2.8833 ± 0.1522 N = 22	2.8661 ± 0.1057 N = 19	2.8902 ± 0.2198 N = 22

TABLE 4. Effect of hydrocarbon-contaminated sediments on water and energy reserves in the muscle of flounder. E1–E5 = treatments; $*P <$ 0.05 between control and treatment.

	Control	E1	E2	E3	E4	E5
Protein (% dry wt.)	94.1900 ± 0.6957 N = 9	93.4340 ± 1.2426 N = 5	94.8 ± 0.67 N = 5	93.6340 ± 0.8219 N = 5	93.6380 ± 1.2221 N = 5	92.321 ± 0.9949* N = 10
Water (%)	83.0565 ± 0.4281 N = 23	83.5917 ± 0.3559 N = 24	82.3579 ± 0.233 N = 22	83.0000 ± 0.3575 N = 22	82.3579 ± 0.3473* N = 19	82.7095 ± 0.3367 N = 22
Lipid (g/100 g wet wt.)	0.9960 ± 0.1378 N = 10	0.8567 ± 0.1394 N = 9	0.784 ± 0.1211 N = 10	0.9144 ± 0.1236 N = 9	0.926 ± 0.1097 N = 10	0.952 ± 0.1154 N = 10
Glycogen (mg/g wet wt.)	1.1585 ± 0.1609 N = 9	1.2151 ± 0.2672 N = 10	0.9526 ± 0.0916 N = 10	0.9472 ± 0.2117 N = 9	1.1053 ± 0.1436 N = 10	0.8353 ± 0.1313 N = 10
Glucose (mg/g wet wt.)	0.1663 ± 0.0224 N = 10	0.1419 ± 0.0175 N = 10	0.163 ± 0.0163 N = 10	0.1324 ± 0.0105 N = 10	0.1945 ± 0.0347 N = 10	0.1756 ± 0.0221 N = 10

which were contaminated with the two highest levels of petroleum were similar at the end of the experiment.

Summation of GC–MS determined naphthalenes, fluorenes, dibenzothiophenes, and phenanthrene/anthracenes (parent and alkylated compounds) gave a total PAH content of approximately 15 mg/g (Table 2). HPLC gave a good approximation of the levels obtained by GC–MS, the concentrations of two-, three-, and four-ring aromatics being 10, 1.8, and 1.3 mg/g, respectively, for a total concentration of approximately 13 mg/g.

Effects on Flounder of Exposure to High Levels of Hydrocarbons (Treatments E3–E5)

The indices investigated ranged from such sensitive biochemical responses as effects on enzyme induction to effects on energy reserves and condition indices. Body condition index or gonad/body weight ratios of flounder were similar at all exposure levels (Table 3). Given the importance of condition indices in assessing the health and well-being of fish populations, the observation that these ratios were little affected, even at the highest exposure levels, is of interest. Little change was also found in muscle concentrations of either protein, lipid, or glycogen and water in petroleum-exposed fish in comparison with controls (Table 4). Besides lack of evidence of body wastage, the fact that energy reserves in muscle tissues were essentially unchanged also indicates minimal differences in metabolic rate such as that associated with the increased stress of "flight and fright" type reactions mediated by the pituitary–interrenal axis (e.g. Wedemeyer et al. 1984).

The important toxicological end points of liver hypertrophy (Table 3) and fatty liver (Table 5) were pronounced at the highest exposure level. Exposure of rats to relatively high levels of drugs and chemicals (especially, but not exclusively, potent MFO enzyme inducers) can lead to liver hypertrophy or fatty liver or sometimes both (Schulte-Hermann 1974). Fletcher et al. (1982) observed an approximate doubling of liver size in flounder exposed to high levels of hydrocarbon-contaminated sediments and recent field studies have demonstrated increased liver size in fish taken from rivers having relatively high levels of mixed organic contamination (Sloof et al. 1983; Fabacher and Baumann 1985). Is liver hypertrophy of toxicological significance? Liver hypertrophy can be an acute and essentially reversible response and thus is often presumed to be of little consequence. However, it is hypothesized that liver hypertrophy and/or fatty liver, which is both pronounced and prolonged in fish, can be reasonably assumed to represent biological harm. One of the best models for this comes from human toxicology and the noted change in liver size and fat content associated with chronic exposure to high levels of alcohol, which may translate (if prolonged) into extensive cirrhosis and sometimes carcinogenesis (Lieber 1984).

A concept sometimes used in chronic toxicity testing with small manmmals to set the upper limit of contaminant exposures suggests that extensive liver hypertrophy and/or fatty liver

TABLE 5. Effect of hydrocarbon-contaminated sediments on energy reserves in the liver of flounder. E1–E5 = treatments; *P < 0.05 between control and treatment.

	Control	E1	E2	E3	E4	E5
Lipid (g/100 g wet wt.)	5.0310 ± 0.4516 $N = 9$	5.4833 ± 0.6886 $N = 9$	5.5956 ± 0.4786 $N = 9$	6.025 ± 0.5981 $N = 5$	6.3556 ± 0.4947 $N = 9$	6.7244 ± 0.7371 $N = 9$
Glycogen (mg/g wet. wt.)	5.0971 ± 1.4883 $N = 6$	9.0176 ± 1.4651 $N = 6$	8.8186 ± 1.3611 $N = 6$	7.5143 ± 1.8473 $N = 6$	12.2375 ± 2.557* $N = 6$	13.0411 ± 2.43* $N = 6$
Glucose (mg/g wet wt.)	0.316 ± 0.042 $N = 5$	0.420 ± 0.046 $N = 6$	0.399 ± 0.057 $N = 6$	0.268 ± 0.58 $N = 5$	0.374 ± 0.042 $N = 6$	0.429 ± 0.025 $N = 6$

TABLE 6. Effect of hydrocarbon-contaminated sediments on induction of MFO (ethoxyresorufin dealkylase) in flounder. E1–E5 = treatments; units are in pmol·mg protein^{-1}·min^{-1}; *$P < 0.05$ between control and treatment.

	Control	E1	E2	E3	E4	E5
Liver	0.1575 ± 0.0311 $N = 21$	0.293 ± 0.0355* $N = 23$	0.8414 ± 0.0986* $N = 22$	0.8709 ± 0.1398* $N = 22$	1.2379 ± 0.1702* $N = 19$	1.0967 ± 0.2* $N = 21$
Kidney	0.1242 ± 0.02 $N = 22$	0.1944 ± 0.0562 $N = 24$	0.2577 ± 0.0404 $N = 23$	0.622 ± 0.1352* $N = 23$	6.5537 ± 1.2135* $N = 19$	8.9161 ± 1.3688* $N = 22$

may indicate genuinely harmful effects. This concept assumes that liver hypertrophy and MFO enzyme increase represent important detoxification processes until the "point of crossover" at which liver hypertrophy continues and MFO enzyme activity begins to decrease (Hutt 1985). It is reasoned that at this critical point, detoxification capacity may become saturated, leading to production of serious secondary pathologies (which are unwanted confounding factors in carcinogenesis testing, but otherwise important indicators of levels of chemicals which may cause genuinely harmful effects). It is interesting that this crossover point was apparently reached at the higher exposure level. That such a crossover point can reasonably be assumed to be associated with impaired health was supported in our study because the higher exposure levels were not only associated with marked changes in liver size and fat content, but also a distinct reduction in spleen size. Overall, our observations suggest that the crossover point concept could be a promising tool for assessing the levels at which inducing chemicals may produce genuinely harmful effects in fish.

Concentrations of chemicals used in laboratory studies are only of importance if they have environmental relevance (a point now widely regarded as being too often disregarded in many past studies). Caution must be exercised in comparing results from different studies on hydrocarbon or PAH levels in waters and sediments because methodologies differ. Further, in the case of mixed hydrocarbon pollution from petroleum and combustion sources, it is difficult to assess bioavailability differences (e.g. Farrington 1986). Bioavailability is commonly discussed in relation to desorption from sediments but desorption of PAH from ingested particles of different types and sizes can be expected to be equally complex. In relation to biological effects the more highly alkylated PAH complexes from petroleum may not be as toxic as the lesser or nonalkylated congeners from combustion sources, or vice versa. Similarly, both petroleum and fossil fuel combustion by-products, which can be expected to be the primary sources of anthropogenic hydrocarbons in coastal waters, contain varying levels of N-, O-, and S-substituted PAH. A large number of studies have described hydrocarbon levels in waters and sediments but it is generally not possible to discriminate between concentrations of aromatics or aliphatics or how much of the aliphatic component is natural in origin. However, a number of studies have now documented levels of PAH in the environment at concentrations similar to the higher levels to which the flounder in this study were exposed. This includes sediments near heavily developed or industrialized areas in the Mediterranean (Mille et al. 1982, 1985), the Charles River, United States (Laflamme and Hites 1978), Norway (Bjorseth et al. 1979), the Neckar, Rhine, and Danube rivers (Hagenmaier and Kaut 1981), the Severn Estuary (John et al. 1979), Casco Bay (Larsen et al. 1983), and oil rig sites in the North Sea (Davies et al. 1984). Very high concentrations of petroleum hydrocarbons will also likely be found for some time in intertidal or nearshore sediments impacted by major oil spills, especially in low-energy environments (Vandermeulen et al. 1981). Measurement of concentrations of single PAH such as benzo[*a*]pyrene can also be useful indicators of total levels of PAH which should in general be at least one or two orders of magnitude higher. In this regard it is worth noting that concentrations of benzo[*a*]pyrene in sediments have been determined at levels of 2–70 μg/kg in South Georgia, Antarctica (Platt and Mackie 1979), 300–1700 μg/kg in Lake Grosser, Federal Republic of Germany (Grimmer and Böhnke 1975), 10–3000 μg/kg in the Bay of Naples (Bourcart and Mallet 1965), 0.5–1700 μg/kg in the Channel and Atlantic coasts of France (Mallet and Letheule 1961), and 180–260 μg/kg in Coria Bay, Australia (Bagg et al. 1981). Such concentrations of benzo[*a*]pyrene should translate into total PAH levels equal to, or much greater than, the higher levels to which the flounder in this study were exposed. It is well known that the ratio of individual or (total) parental PAH to total PAH (which also includes various alkylated homologs) is low in petroleum and petroleum combustion by-products (e.g. Boehm 1983). For instance the ratio of parental phenanthrene/anthracene to total PAH in Venezuelan crude is approximately 1:50 (Table 2).

Overall, the results obtained in this study with winter flounder indicate that many point sources of sediment hydrocarbon contamination worldwide, such as in the immediate area of oil rigs, sewage outfalls, oil refineries, or countless numbers of highly polluted harbors, estuaries, and rivers, are probably deleterious to fish health.

Results of this subchronic toxicity study also point to the importance of exercising caution when using the popular index

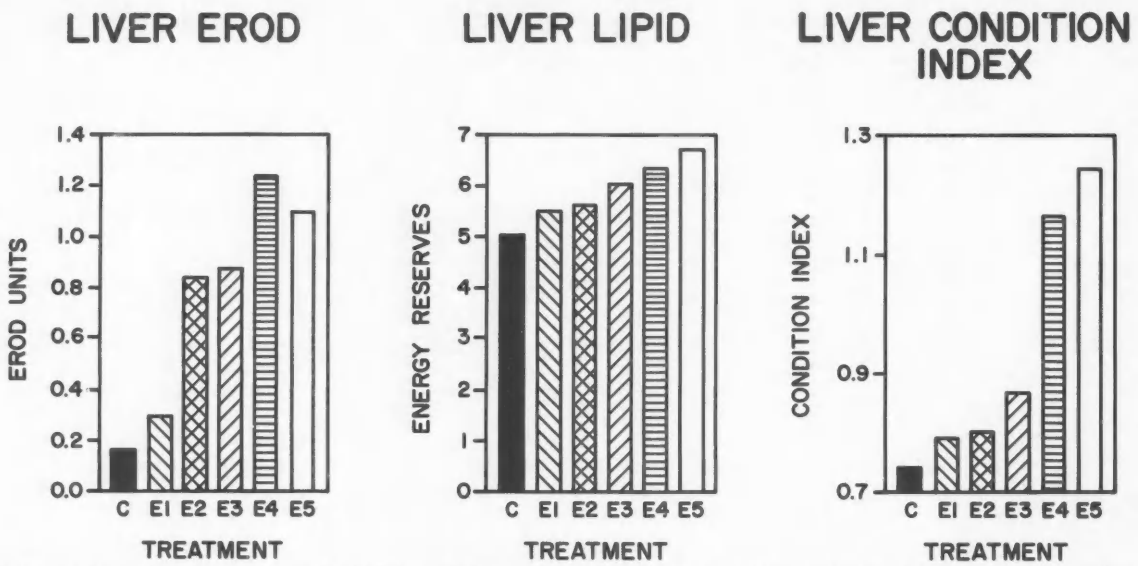

FIG. 1. Demonstration of stepwise trend in liver hyperplasia, fatty liver, and MFO enzyme induction in flounder exposed to hydrocarbon-contaminated sediments.

of increase in blood glucose, or its counterpart, decrease in tissue glycogen in assessing contaminant-induced stress (Wedemeyer 1977). Both of these can be considered to be excellent indicators of "flight and fright" type stress typified by increase in metabolic rate and an enhanced rate of depletion of energy reserves but are not suitable indicators of subtler types of cell and tissue impairment. For instance, in this study with flounder, levels of glycogen in liver were markedly increased rather than decreased by exposure to hydrocarbons (Table 5).

Effects of Exposure to Low levels of Hydrocarbons (Treatments E1–E2)

In addition to the more pronounced effects noted at the higher levels of exposure, effects were also noted at the lower levels including the lowest. This included an increase in levels of MFO enzymes (Table 6) as well as small increases in the toxicologically important end points of liver hyperplasia (Table 3) and fatty liver (Table 5). Changes in liver size and fat content were not statistically different from controls in fish exposed to the lower hydrocarbon levels but a stepwise trend was apparent, beginning with the lowest level of contamination. This stepwise trend in liver hyperplasia, fatty liver, and MFO enzyme induction is illustrated in Fig. 1.

Slight changes in biological, and especially biochemical indices, may not be indicative of adverse health effects, and a critical question in toxicology is assessing the degree of change that may really be harmful. This assessment is essentially judgmental. We have reasoned that prolonged and large changes in liver size and fat content are probably indicative of genuine harm for fish, but are small changes in such effects harmful, even if prolonged? By analogy as previously noted in the case of the human model for alcoholism, it can be stated that large changes in liver size and fat content are harmful, but can the term harmful be ascribed to small incremental changes which may be produced by "normal" alcohol consumption? (Such questions are difficult to answer, since it is akin to determining whether a person's normal ageing, cancer, or arteriosclerosis rate is increased by days, weeks, months, or years (if at all) by exposure to trace levels of natural or anthropogenic sources of PAH in food, not to mention the conundrum of dietary insufficiencies or natural food toxicants which could be much more important factors in influencing the etiologies of these diseases in the first instance.)

In our study with winter flounder, the important toxicological end points of liver hypertrophy and fatty liver, which have been associated with the carcinogenic potential of many chemicals, began to appear at the lowest exposure levels. Bannasch et al. (1980) documented that the development of liver tumors in experimental animals often appears to be preceded by hepatocellular glycogenosis. This is of interest because an increase in liver glycogen levels was noted at the lowest level of hydrocarbon exposure. Indeed, following the argument that MFO enzyme induction, liver hypertrophy, and glycogenosis are important indicators of carcinogenicity (Schulte-Hermann 1985), it is tempting to speculate that even very low levels of PAH in sediment may be signalling a "carcinogenic potential"; however, one should use such terms with caution. Also, as noted above, any presumed slight risk of carcinogenesis or other types of toxicity due to a pollutant may be small or insignificant if compared with the importance of malnutrition, undernutrition, natural toxicants in food, or such factors in combination in modulating the same toxicological end points.

Whatever the judgment as to the possible significance of small changes in toxicologically important end points, the fact that very low levels of PAH in sediments are bioavailable in sufficient concentration to effect any biological change is of special interest. As discussed above, there are likely many point sources of hydrocarbons worldwide where levels in sediments may be bioavailable to a sufficient degree to be harmful to fish. However, regardless of the local importance of such pollution, areas identified as potentially harmful are in general restricted to heavily developed or industrialized areas. Any potential for more broad-scale effects in the marine environment would obviously be of greater interest and this study indicates such a

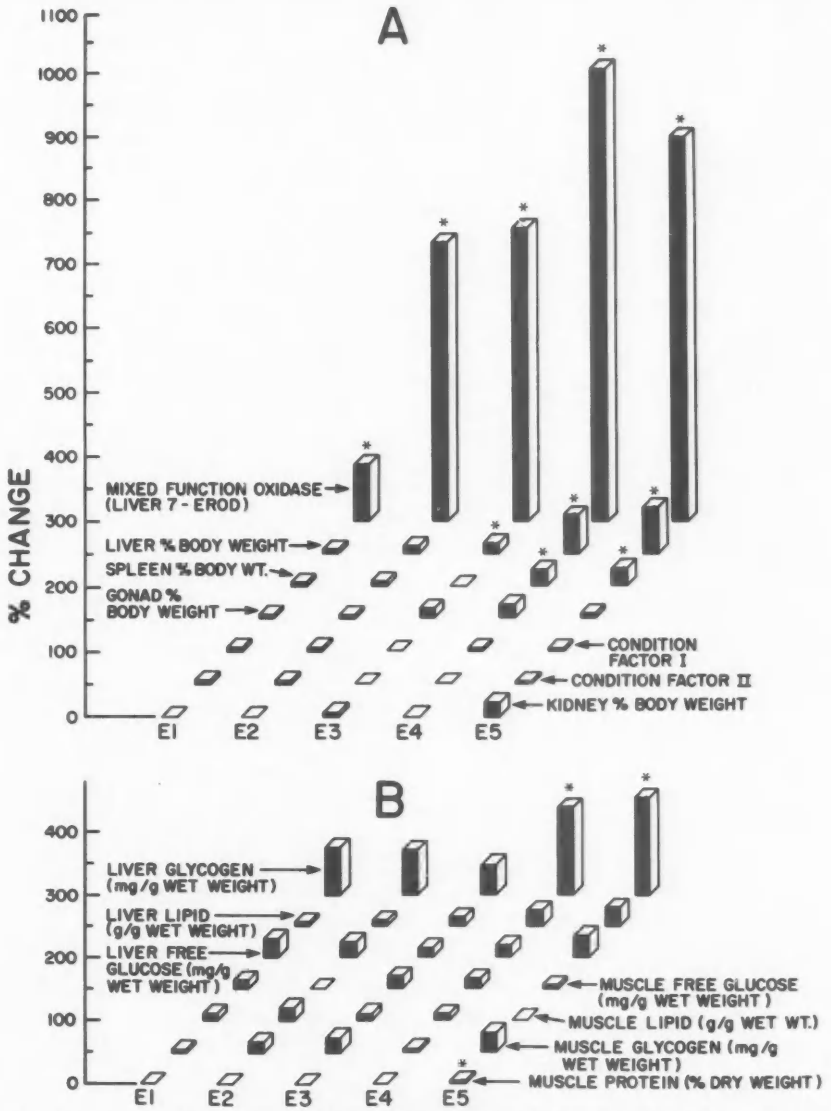

FIG. 2. Percentage change in various indices in flounder chronically exposed to different levels of sediment hydrocarbons (*$P < 0.05$). E1–E5 represent different dose levels. (A) Biological indices: condition factor I is in terms of total body weight and condition factor II is in terms of gonadectomized body weight; similar results were obtained in terms of carcass weight (not shown). (B) Biochemical indices.

possibility. Caution must be exercised in comparing results from different studies; however, it is worth noting that PAH levels in the 0.1 to 5.0 parts per million range (100–5000 μg/kg) have been reported in the New York Bight (Laflamme and Hites 1978), Buzzards Bay (Youngblood and Blumer, 1975; Hites et al. 1977), Massachusetts Bay (Windsor and Hites 1979), the Baltic Sea (Poutanen et al. 1981; Law and Andrulewicz 1983), and the Cariaco Trench (Laflamme and Hites 1978; Johnson et al. 1985). Similarly, concentrations of aromatics in coastal sediments (aromatics or benzene eluates from column chromatography) have been determined at levels of 1.8–2.6 μg/g in Mississippi, Alabama, and Florida (Gearing et al. 1976), 10 μg/g in southern Texas (Sever 1970; Lytle et al. 1973), 1.7–19.9 μg/g in northern Texas and western Louisiana (Stevens et al. 1956), and 1.5–9.3 μg/g in the North Atlantic (Farrington and Tripp 1977). By comparison, with these various studies, effects were noted in flounder at similar or lower levels of hydrocarbon exposure (~1.0 μg/g).

This indicates that in addition to the many point sources of hydrocarbon contamination throughout the world, where genuine harmful effects to fish can be presumed possible, there may exist much wider geographical areas where effects may be

possible, albeit difficult, at this juncture to ascribe the term harmful.

The most distinct change in flounder noted at the lower level of exposure was induction of the MFO enzyme system. This system plays an important role in detoxification, transforming foreign compounds (which may include many natural dietary constituents) into derivatives more easily eliminated from the organism. However, some compounds can be activated to reactive, more toxic species which may otherwise be generally cytotoxic, mutagenic, or carcinogenic (e.g. see reviews by Bend and James 1978; Stegeman 1981; Conney 1982; Lech et al. 1982; Payne 1984). Most interest to date has centered around a role for MFO in increasing or decreasing certain types of chemical carcinogenesis, but the MFO enzyme system may play a primary role in various types of chemical toxicity, e.g. cataract formation (Nebert and Jensen 1979), retinal degeneration (Hitoshi et al. 1976), atherosclerosis (Majesky et al. 1983), and immune function (Silkworth et al. 1984). There is also recent evidence that metabolic pathways involving cytochrome P-450 enzymes may initiate or modulate damage due to oxygen radicals which are believed to play a key role in a wide spectrum of chemical induced toxicities including carcinogenesis (Gonder et al. 1985). Similarly, because steroid compounds are "natural" substrates for MFO enzymes, physiological functions such as reproduction may be affected in animals subjected to artificially high levels of inducing chemicals (Truscott et al. 1983; reviewed by Khan 1984; Spies et al. 1984). Thus, in view of the mounting evidence for the fundamental importance of MFO in modulating (increasing or decreasing) a variety of toxicological end points, the MFO enzyme activity changes noted in this study at the lowest levels of hydrocarbon exposure are of special interest.

One of the primary interests which have developed in aquatic toxicology over the past few years has been use of the induction of MFO enzymes in fish as a sensitive biochemical indicator for use in biological monitoring and assessment studies (e.g. see reviews by Payne 1984; Addison 1984; Payne et al. 1987). Our study has established dose–response relationships for hydrocarbons in sediments, and induction was observed at very low concentrations of sediment hydrocarbons, much lower than those required for the production of toxicological end points believed to represent biological harm (at least in the short term). The relative sensitivity of MFO enzyme induction is demonstrated in Fig. 2. These observations support the hypothesis that from a regulatory or environmental management perspective, one of the primary values of such sensitive responses as MFO enzyme induction is as early warning indicators in defining boundary limits for point sources of pollution such as oil spills.

General Discussion

Are There Threshold Levels of PAH in Water or Food for Effects on Fish?

The results obtained with low levels of hydrocarbons in sediments lead to equally interesting speculations about the potential for similar if not enhanced sublethal effects in water column dwelling species. It is reasonable to assume that sediment hydrocarbons enter fish principally through ingestion of interstitial waters containing PAH adsorbed to particulate matter. By comparison, soluble levels which might slowly elute from sediments and enter fish via gills or skin, if at all, should be extremely low. (Note that Thomas and Rice (1982) found little evidence for the transport of relatively insoluble PAH across gill tissues in fish.) The fish in the present experiment were approximately 200 g, and if we assume that the rate of water ingestion in winter flounder is similar to starry flounder (*Paralichthys lethostigma*) (Hickman 1968), this could result in the ingestion of approximately 25 mL of water per day per fish. If it is further assumed that the ingestion of 25 mL of water results in the ingestion of 25 mg of sediment, the lowest concentration of hydrocarbons to which the fish were exposed (~1.0 μg/g) would result in the introduction of approximately 0.025 μg of PAH per day per fish. This amount of sediment ingestion is probably a large overestimate because such an amount or even much less would have lead to readily detectable levels (25 mg × 100 = 2.5 g over a 100-d period) in the stomach. It is also worth noting that PAH may be poorly absorbed from the digestive tract of fish even when dissolved in a vehicle such as herring oil (Niimi and Palazzo 1986). Thus, absorption of PAH from sediments would be expected to be further greatly decreased (in comparison with unadsorbed PAH in the digestive tract), minimizing the actual "dose" available. Compared with flounder, a 200-g water column dwelling fish ingesting 25 mL water/d containing 1 μg PAH/L would ingest 0.025 μg of hydrocarbons, approximately the level consumed by the flounder at the lowest exposure levels in this study. It is reasonable to assume that water-accommodated hydrocarbons may be bioavailable to a greater degree (in terms of transport across the gut) than hydrocarbons adsorbed to small sediment particles. By comparison, aromatics in the 1 μg/L range or greater have been reported in surface or subsurface waters of the New York Bight, the Virginia Capes, the western Sargasso Sea, and the Caribbean Sea (Brown et al. 1973), Lake Maracaibo, Venezuela (Battelle 1974), and San Francisco Bay (DiSalvo and Guard 1975).

In some cases, fluorimetric techniques have been used to measure hydrocarbons in water. Bunker C equivalents (which can be assumed to contain aromatics in the 20% range) have been detected at 1.5–4.2 μg/L in subsurface waters of the Gulf of St. Lawrence, Canada (Levy 1971), 1.9–5.5 μg/L in the St. Lawrence River, and 1.6–13.5 μg/L off Nova Scotia. Concentrations of hydrocarbons in surface microlayers can be expected to be much higher. For instance, Levy (1986) reported hydrocarbon concentrations from 4.5 to 20.9 μg/L in the surface microlayer and 0.57 μg/L in the water column on the Labrador Shelf in 1983. Similarly, Gordon and Keizer (1974) measured Venezuelan crude oil equivalents in the relatively pristine waters on the Grand Banks of Newfoundland at concentrations up to 39 μg/L, and since the level of aromatics (two rings and larger) in Venezuelan crude oil is approximately 1.55, this translates into 0.5 μg total aromatics/L. Due to the relatively high fluorescence yield of complex mixtures of petroleum hydrocarbons versus combustion hydrocarbons, calibrations on the basis of crude oil equivalents can lead to an underestimation of total PAH levels, should the PAH principally be from combustion sources. On the other hand, reliance on fluorimetric techniques for the measurement of anthropogenic hydrocarbons should be approached with caution, since natural products may have qualitatively similar fluorescence spectra.

A case for finding sublethal effects of hydrocarbons over relatively large geographical areas can possibly be best made for fish populations in the Mediterranean Sea and Arabian Gulf. Ravid et al. (1985) reported that all areas of the eastern Mediterranean are contaminated by aromatic hydrocarbons, with concentrations from about 0.3 to ≥ 40 μg/L. Also, the

mean concentrations of hydrocarbons found in the seawater of Kuwait (2.95 μg/L), Saudi Arabia (4.14 μg/L), and Qatar (3.29 μg/L) have led to the hypothesis that the northwestern part of the Arabian Gulf is more highly polluted than other marine environments including the Mediterranean (El Sambra et al. 1986). The Gulf is a relatively shallow and isolated sea and our results suggest that effects such as MFO enzyme induction, liver hyperplasia, and fatty liver may be common in fish populations in the Arabian Gulf. It is also less likely that any putative hydrocarbon-mediated effects found in fish in the Gulf would be confounded by the presence of relatively high or "extreme" concentrations of other contaminants, the situation in such areas as the New York Bight, the German Bight, Chesapeake Bay, and certain regions of the Great Lakes. This makes the Arabian Gulf an attractive site for addressing concerns related to petroleum hydrocarbon pollution and animal carcinogenesis.

We also introduce the possibility that tar balls and flakes which are often found in surface waters in relatively high amounts (Clark and MacLeod 1977) may also be a source of hydrocarbons of some biological significance. It is generally assumed that due to the nature and surface association of these particles, they may be of little toxicological significance for fish. However, it is likely that large amounts of surface particles will be mixed into subsurface waters under storm conditions, and this mixing could be particularly important in shallow seas. Furthermore, tar balls and flakes are relatively pure forms of high molecular weight hydrocarbons and their congeners (enriched in PAH) (Clark and MacLeod 1977; Jordan and Payne 1980) and could be much more bioavailable to fish (if ingested) than, for instance, the relatively low levels of PAH adsorbed to sediment particles.

Food could also be an important source of PAH for fish; our results with flounder support the hypothesis that levels of PAH found in prey could sometimes be sufficient to cause biological changes in fish. Mussels contaminated with 20 μg benzo-[*a*]pyrene/kg or higher (200–500 μg/kg in some instances) have been reported from a number of inshore waters including France (Perdriau 1964; Bourcart and Mallet 1965), Italy (Bourcart and Mallet 1965; Fossato et al. 1979), the United States (Mix et al. 1977; Mix and Schaffer 1983; Gossett et al. 1983), and Canada (Picard-Berube et al. 1983). Even if we consider the lower limit of 20 μg benzo[*a*]pyrene/L, this could translate into one to two orders of magnitude or 200–2000 μg PAH/L. The consumption of 50 g of such contaminated mussels per day could result in the ingestion of PAH in the 10–100 μg range. By comparison, an upper limit of 0.025 μg PAH/d might be available to fish exposed to the lowest levels of sediment hydrocarbons. Likewise, can we extend the hypotheses for possible effects not only in coastal waters, where point sources may be numerous but localized, but to offshore areas, such as regions of commercial fisheries? Boehm (1980) has reported petroleum hydrocarbon concentrations in the 200 μg/g range in several species of fish in the Gulf of Mexico, including butterfish, flounder, lizardfish, porgy, scad, snapper, and spat. Preliminary studies by Zitko (1975) also point to the need for determining hydrocarbon levels in fish and invertebrates in Canadian coastal waters.

In summary, on the basis of observations in this study with flounder, it can be hypothesized that PAH may be commonly found in the environment at levels which can produce biological effects in fish. In addition to localized areas of contamination, we suggest that the case for finding sublethal effects over relatively large geographical areas can possibly be best made for fish populations in the Mediterranean Sea and Arabian Gulf. Further, individual sources could commonly include waters and prey species as well as sediments. It is understood that depending on locale, PAH contamination could be either from petroleum or combustion sources (perhaps more commonly mixtures of the two) and the more highly alkylated PAH compounds in petroleum may have a greater or lesser toxicity potential than PAH from combustion sources.

The No-Effect Level Dilemma

There is an evolving environmental ethic concerning the importance of not only obtaining "toxicity-free" effluents but also restoring polluted waterways and reservoirs to their natural "nontoxic" state. (For instance, lobsters found in Sydney Harbor in Nova Scotia, Canada, are contaminated with relatively high levels of PAH (Uthe and Musial 1986) and there is presently a major effort to clean up the waterway.) This study demonstrates that an interesting dilemma would arise if agencies were to advocate safety factors similar to those often used for the promulgation of guidelines, advisories, or regulations for many drugs and chemicals. For instance, a 100:1 safety factor has a relatively strong basis in the biological sciences, and this factor has been modified in FDA regulations and remains in widespread use throughout the world for all toxicants that have a threshold for effects (the so-called no observable effect level or NOEL) (Hutt 1985). Given the very low levels of sediment PAH which produces sublethal effects in flounder (excluding the extrapolation for PAH exposures by the water column and food), the difficulty of arguing for a 1:1 safety factor, let alone 10:1 or 100:1, for PAH contamination from such sources as sewage outfalls, hydrocarbon development areas, or marine dump sites would present a dilemma when similar or even much higher levels of PAH may be common, not only at point sources, but over wide-scale geographical areas in association with the burning of forests and grasslands, natural oil-seeps, and myriad numbers of smokestacks. Indeed a 10:1 to 100:1 safety factor would be in general conflict worldwide with levels of PAH from natural combustion sources and natural oil-seeps which have existed over geological time. This demonstrates the importance of maintaining a scientific perspective for regulating effluents or restoring polluted waters. It also highlights the importance of establishing criteria in toxicology (in general and aquatic toxicology in particular) for distinguishing between "harmless" and harmful sublethal effects.

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Seasonal Variation in Faunal Distribution within the Sediments of a Canadian Shield Stream, with Emphasis on Responses to Spring Floods

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Giberson, D. J., and R. J. Hall. 1988. Seasonal variation in faunal distribution within the sediments of a Canadian Shield stream, with emphasis on responses to spring floods. Can. J. Fish. Aquat. Sci. 45: 1994–2002.

The vertical distribution of invertebrates within the shallow substrates of a Canadian Shield lake outflow stream was examined to determine the importance of season and spate on distribution pattern. Stream invertebrates were found throughout the year to depths of 25 cm below the sediment surface, only about 5 cm above bedrock. Insect abundance showed a strong seasonal pattern, with highest numbers occurring during early winter (December) in all depth zones. Except for Chironomidae, the majority of the insects found below 5 cm were early instar larvae of those found regularly at the surface. Insect abundance was generally higher at the sediment surface than for all other depth zones combined and consisted mainly of one taxon, *Prosimulium* (Diptera: Simuliidae). Non-insect invertebrates were always more abundant in the hyporheos than at the surface. Total invertebrate abundance (primarily *Prosimulium*) at the sediment surface decreased by about 40% during the spring snowmelt flood, but no significant changes in abundance occurred in the hyporheos during this period. Chemical analysis of surface and interstitial water showed that both pH and alkalinity decreased slightly in surface waters during the flood, but increased within the hyporheos, particularly on the rising limb of the flood hydrograph.

La distribution verticale d'invertébrés dans les substrats peu profonds d'un émissaire d'un lac du Bouclier canadien a été examinée dans le but de déterminer l'importance de la saison et des crues sur l'allure de la distribution. Des invertébrés ont été trouvés tout au long de l'année à des profondeurs de 25 cm en-dessous de la surface des sédiments, à seulement 5 cm au-dessus de la couche rocheuse. L'abondance des insectes présentait une allure saisonnière prononcée, les nombres les plus élevés étant notés au début de l'hiver (décembre), dans toutes les zones de profondeur. À l'exception des chironomidés, la majorité des insectes trouvés à plus de 5 cm de profondeur étaient des larves aux premiers stades de croissance des insectes couramment trouvés à la surface. Les insectes étaient généralement plus abondants à la surface des sédiments que dans toutes les autres zones réunies et ceux-ci étaient généralement représentés par un seul taxon : *Prosimulium* (Diptère : imuliidé). Les invertébrés autres que des insectes étaient toujours plus abondants dans l'hyporhéos qu'à la surface. L'abondance totale des invertébrés (surtout les *Prosimulium*) à la surface des sédiments diminuait de 40 % environ au cours de la crue de printemps due à la fonte des neiges, mais aucune modification appréciable de l'abondance dans l'hyporhéos n'a été notée durant cette période. L'analyse chimique de l'eau de surface et de l'eau interstitielle a montré que le pH et l'alcalinité diminuaient légèrement dans les eaux de surface au cours de la crue, mais que leurs valeurs augmentaient dans l'hyporhéos, surtout pendant la période correspondant à la partie ascendante du graphique de la crue.

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The deeper sediments of streams (known as the hyporheic zone; Williams and Hynes 1974) have been suggested as a possible refuge from short-term physical or chemical stresses for stream invertebrates, since recolonization after flooding or pesticide application is often too rapid to be attributed to downstream drift or upstream migration alone (Williams and Hynes 1976; Williams 1984). Vertical migrations from the hyporheos into the surface layers after a flood have been recorded by Williams and Hynes (1976) and there is some evidence for directed movements deeper into the substrate during a summer spate (Williams and Hynes 1974). Predictable increases in stream discharge occur regularly in Canadian streams, especially those associated with the rapid melting of snow in spring, but the vertical distribution of the benthos through the stages of a spring flood is not known. The seasonal invertebrate distribution pattern within the sediments of Precambrian (Canadian) Shield streams is also poorly known, largely due to problems in sampling these habitats. In contrast with more conventional streams that possess deep, well-drained gravel substrates, substrates in many shield streams are shallow and consist of large angular materials overlying granitic bedrock, making sampling difficult.

This study is part of a larger study of the distribution of stream invertebrates in acid-impacted streams in central Ontario. The

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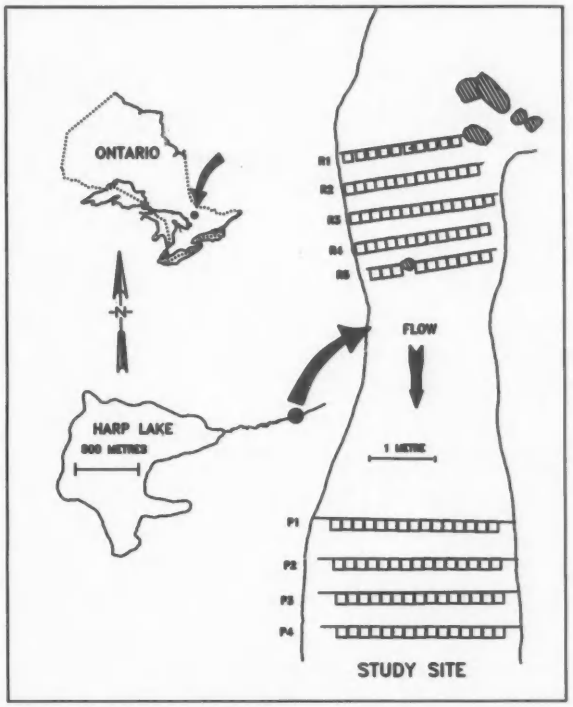

FIG. 1. Study site and distribution of surface substrate baskets along transects in each of the riffle (R) and pool (P) reaches of Harp Lake Outflow, October 1985 – June 1986.

area in which the study stream is located receives significant inputs of acid precipitation (pH $\simeq$ 4.2; Dillon et al. 1978), but the study stream itself is not considered to be acid impacted. The objective of the study was to provide baseline data on the seasonal and spring flood vertical distribution patterns of selected abiotic (pH, alkalinity, and dissolved oxygen) and biotic (invertebrate abundance) parameters in sediments of a non-acid-impacted stream.

Study Site

Harp Lake outflow is located near the town of Huntsville in south-central Ontario (45°23′N, 79°08′W; Fig. 1). Riparian vegetation is primarily beech–maple (Seip et al. 1985), and the study stream possesses a shallow substrate overlying granitic bedrock (details of catchment geology and soil geochemistry are provided in Jeffries and Snyder 1983). The mean annual pH during 1982–86 was 6.3 (range 5.7–6.8) and the mean alkalinity was 3.3 mg (65.9 μeq) $CaCO_3$/L (range 1.4–4.2 mg/L (28–84 μeq/L) (P. Dillon, Dorset Research Station, Dorset, Ont., unpubl. data).

The study site was 500 m downstream of the lake outlet and consisted of a riffle reach (~2 m wide × 4 m long × 10–15 cm deep at low water) with a pool (~3 m wide × 5 m long × 60–75 cm deep) immediately downstream (Fig. 1). Substrate depth averaged about 30 cm in both reaches, although it was more variable in the pool due to deposition and scouring of fine materials associated with variations in stream discharge. The substrate in both zones consisted of large (up to 0.5 m diameter) angular pieces of granite interspersed with smaller pieces (~ 0.1 m diameter). The large interstitial spaces were filled with gravel and sand. During low water periods the large mineral sediments in the pool zone were overlain by varying amounts of sand and organic debris.

Methods

Invertebrate Sampling

Invertebrates were sampled at 2- to 3-mo intervals from October 1985 to June 1986 to establish the seasonal pattern of vertical distribution within the sediments. Sampling frequency was increased to 2-wk intervals from the beginning of March to assure an adequate preflood sample and then at 0, 1, 4, 8, and 24 d after the onset of flooding to obtain flood and postflood samples. Consequently, many more samples were collected in the spring than at any other time of year. The following sampling periods were designated for the analysis of seasonal distribution: fall, 17 October 1985; early winter, 12 December 1985; late winter, average of samples collected on 11 March and 26 March 1986; flood period, average of samples collected 31 March, 1 April, 4 April, and 8 April 1986; spring, 24 April 1986; and early summer, 12 June 1986.

Hyporheic invertebrate densities were sampled by the standpipe corer of Williams and Hynes (1974) modified for use in the shallow substrates of Harp Outflow. Five 25-mL samples were collected at two depths (10–15 and 20–25 cm) in each reach on each sampling date. The corer did not sample invertebrate densities at the sediment surface (0–5 cm depth), so these were obtained using artificial substrates. Wire baskets (15 × 15 × 5 cm × 6 mm mesh) were filled with a standardized volume and size selection of in situ substrate materials and imbedded into the substrate. The basket samples were chosen because they allowed an estimate of density per unit volume (for comparison with hyporheic samples) and because preliminary sampling showed that the baskets compared favourably with kick samples in species composition and relative abundances for the same area of stream (D. J. Giberson, unpubl. data). Sixty baskets were placed into each of the riffle and pool zones prior to leaf fall and autumn rains and left to condition for a minimum of 2 mo. Five were collected randomly from each zone on each sampling day. Benthic insects were identified to genus where possible and to major taxonomic grouping for noninsect invertebrates. Samples were converted to numbers per litre to facilitate comparisons between hyporheic and surface invertebrates.

Water Chemistry and Discharge

Surface water samples for chemical analyses were collected weekly during the study period (October 1985 – June 1986). For the snowmelt study (preflood, flood, and postflood periods; 11 March – 24 April 1986), surface and interstitial water samples (Williams and Hynes 1974) were collected at two locations within each zone on each sample date. Alkalinity was determined by Gran titration, pH by a combination glass electrode standardized against appropriate buffers, and dissolved oxygen (DO) by the Winkler titration at the Dorset Research Laboratory. Water temperature was determined from a maximum–minimum thermometer located just upstream of the study site.

Stream discharge was measured upstream from the study area by determining the velocity of the water at 0.1- or 0.2-m intervals from stream bank to bank and combining these measurements with the cross-sectional area of the stream (discharge =

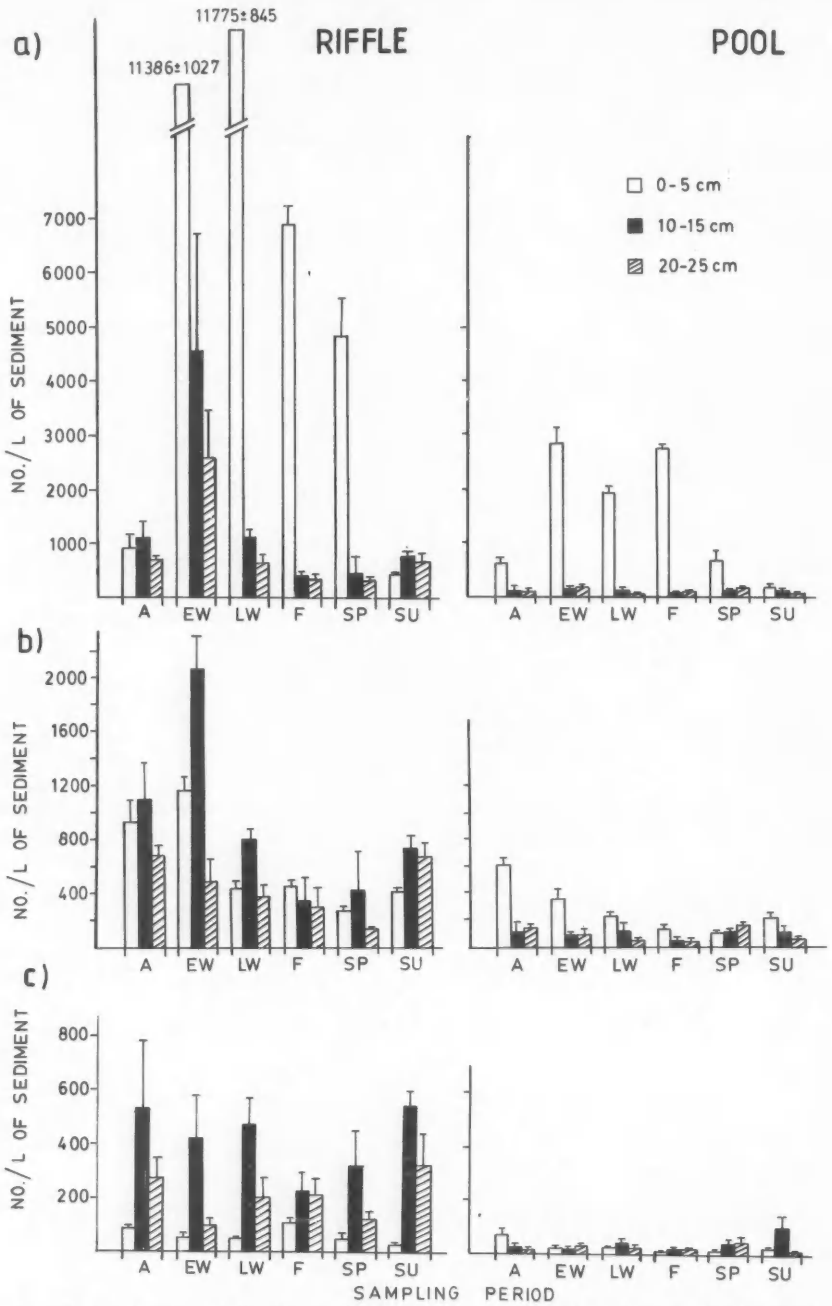

FIG. 2. Seasonal pattern of distribution within the substrates of Harp Lake Outflow, October 1985 – June 1986. (a) Total invertebrate abundance; (b) total invertebrates excluding Simuliidae; (c) Abundance of noninsect invertebrates ($\bar{x} \pm$ SE; note difference in scale). A, autumn (17 Oct. 1985); EW, early winter (17 Dec. 1985); LW, late winter (11 Mar. and 26 Mar. 1986 samples averaged); F, flood period (31 Mar. – 8 Apr. 1986 samples averaged); SP, spring (24 Apr. 1986); SU, summer (12 June 1986).

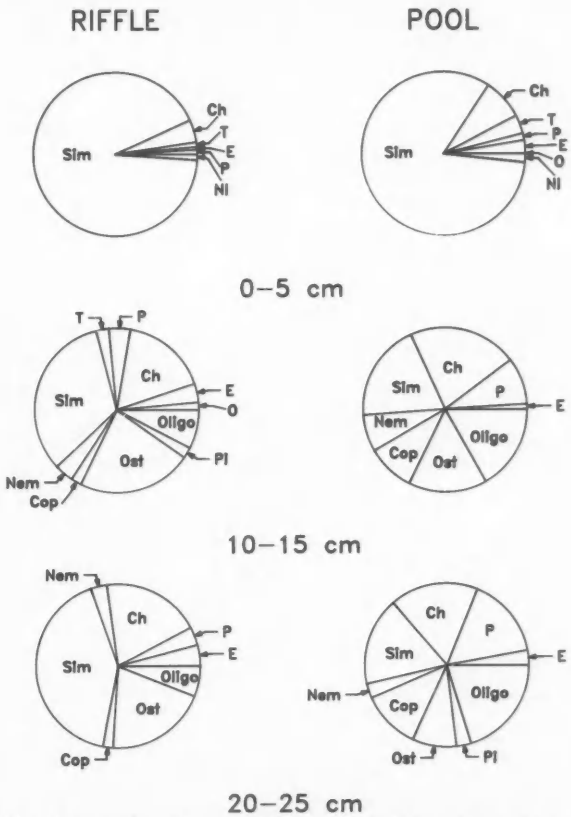

FIG. 3. Proportion of invertebrate groups inhabiting different depth zones in two reaches of Harp Outflow, October 1985 – June 1986. E, Ephemeroptera; P, Plecoptera; T, Trichoptera; Ch, Chironomidae; Sim, Simuliidae; O, other insects; NI, noninsect invertebrates; Ost, Ostracoda; Oligo, oligochaetes; Nem, nematodes; Pi, Pisididae; Cop, Copepoda.

cross-sectional area × velocity). Water velocity was measured with either an Ott or a Teledyne Gurley Pygmy meter.

Results

Seasonal Distribution

Invertebrates

Total invertebrate abundance varied seasonally in all depth zones (0–5, 10–15, and 20–25 cm) and both reaches. Invertebrates were most abundant at the surface (0–5 cm) during the winter months in the riffle reach and during the winter and the spring flood period in the pool (Fig. 2). Total numbers in the hyporheos (10–15 and 20–25 cm depths) reached peak values in the riffle in early winter and were generally low throughout the year in the more unstable pool reach (Fig. 2). Densities within the hyporheos were not related to those at the surface on any given sampling date. However, most insects in the hyporheos at this time were early instar larvae of those found at the sediment surface later in the year (instar analyis was based on wingpad development in hemimetabolous insects and size in holometabolous ones; D. J. Giberson, unpubl. data).

Faunal composition, particularly of the insect taxa, also varied seasonally in all depth zones. Insects were generally

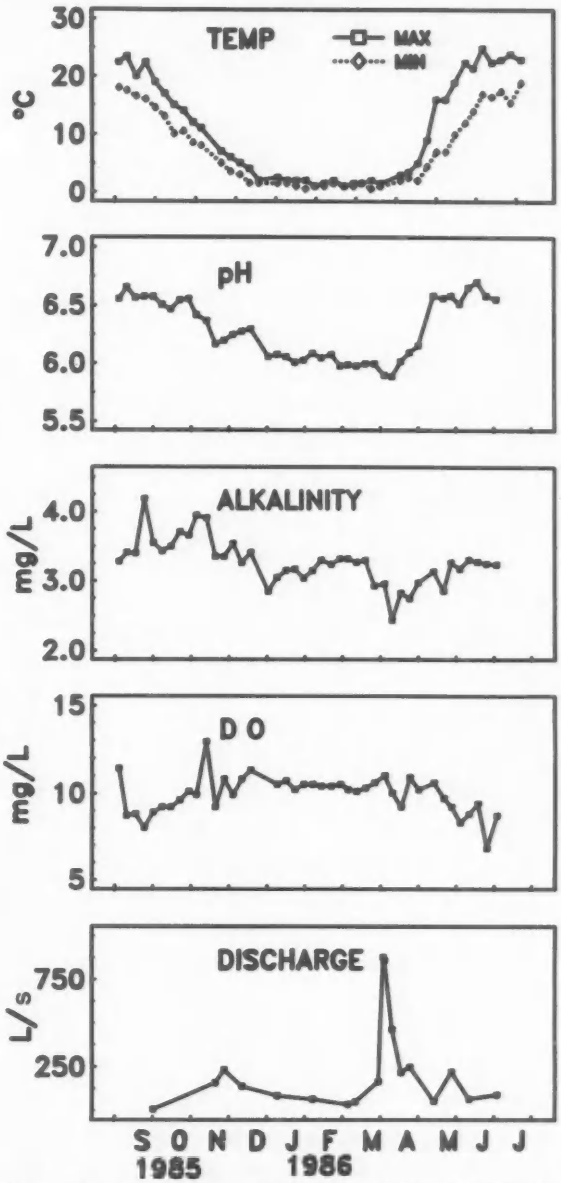

FIG. 4. Physical (temperature and discharge) and chemical (DO, pH, and alkalinity) patterns in Harp Lake Outflow, September 1985 – July 1986.

common in the surface sediments throughout the year, but were only important in the substrate during the fall–winter and early summer recruitment periods (Fig. 2). Noninsect invertebrates, on the other hand, varied little seasonally, but were more common in the hyporheic zone than at the surface (Fig. 2c).

Simuliids, especially *Prosimulium*, comprised about 90% of the total annual surface (0–5 cm) population in both reaches (Fig. 3). The extremely high numbers of blackflies (>600 000/m^2 at the sediment surface during the winter months) obscured the distribution pattern for the other taxa, so vertical distribution was plotted both including (Fig. 2a) and excluding (Fig. 2b)

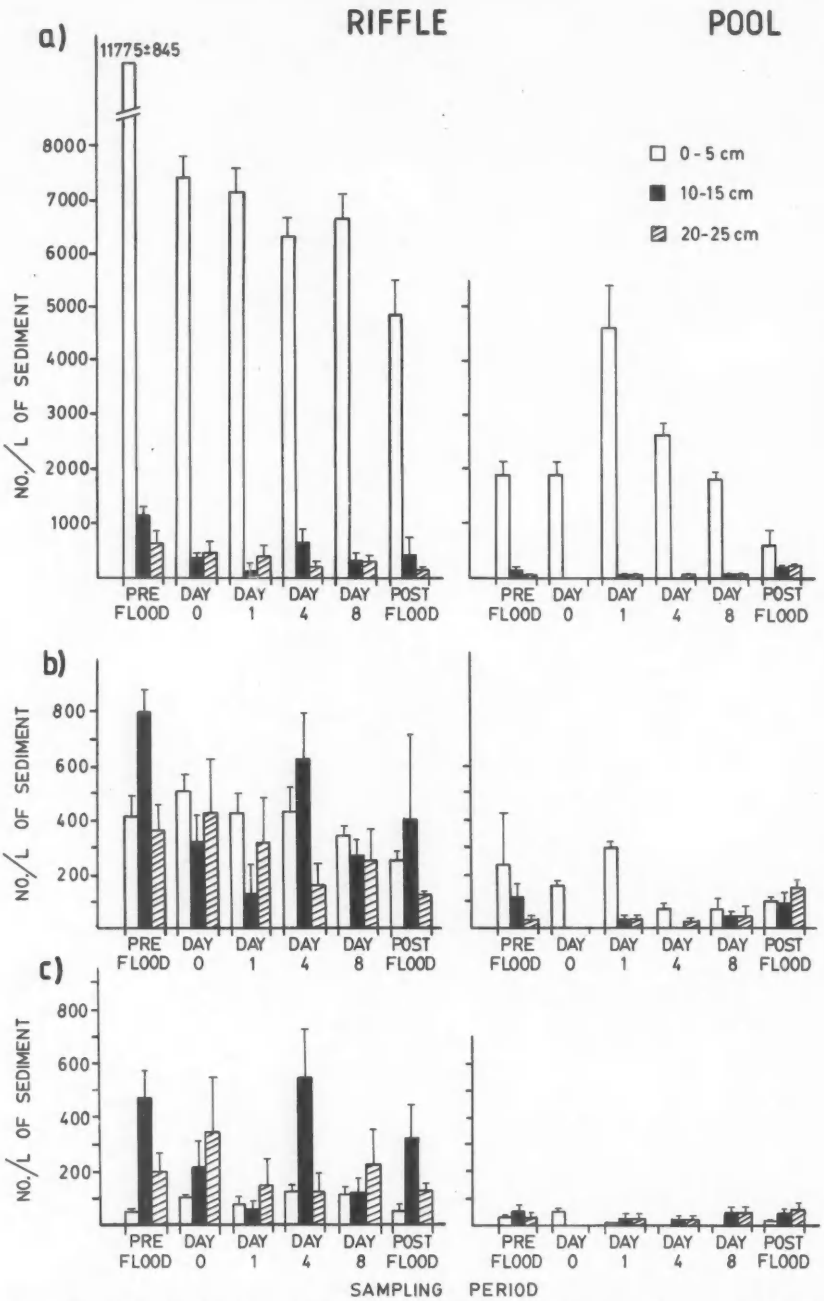

FIG. 5. Depth distribution of invertebrates in Harp Lake Outflow during the spring snowmelt flood, 31 Mar.–8 Apr. 1986. (a) Total invertebrates; (b) total invertebrates excluding Simuliidae; (c) noninsect invertebrates ($\bar{x} \pm$ SE; note difference in scale). Preflood and postflood periods correspond to late winter and spring periods, respectively, from Fig. 2.

the Simuliidae. The peak in surface densities, for example, occurred later (late winter, Fig. 2a) for blackflies than for the remaining invertebrates (early winter, Fig. 2b). The hyporheic zone, on the other hand, showed the same general pattern whether or not blackflies were excluded from the analysis, with a density peak in early winter in the riffle, and no pattern in the pool.

The pattern of vertical distribution varied among the insect orders (Fig. 3), although generally, Diptera (Chironomidae and small Simuliidae) were the most abundant in the hyporheic

TABLE 1. Chemical data for surface and interstitial waters of Harp Lake Outflow, 11 March – 12 June 1986. N/A = no sample collected for that date; ranges given where >1 sample taken. Alk, mg $CaCO_3$/L; DO, mg O_2/L.

		Riffle						Pool					
				Interstitial						Interstitial			
		Water column		10 – 15 cm		20 – 25 cm		Water column		10 – 15 cm		20 – 25 cm	
Date	Parameter	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
11 March	pH	6.04	6.03–6.06	N/A		5.93	5.88–5.96	6.03	6.00–6.06	N/A		6.17	6.13–6.21
	Alk	3.3	3.19–3.49			5.66	4.91–6.41	3.30	3.19–3.49	N/A		9.96	8.86–16.5
	DO	N/A		N/A		N/A		N/A		N/A		N/A	
26 March	pH	5.99	5.97–6.00	6.02	6.00–6.04	6.23	6.22–6.25	5.95	5.94–5.96	5.90	5.80–6.00		
	Alk	3.00	2.97–3.03	4.26	3.36–5.16	12.2		2.81	2.79–2.82	5.62	4.91–6.41	29.0	27.6–30.4
	DO	N/A		N/A		N/A		N/A		N/A		N/A	
31 March	pH	5.93	5.93–5.94	5.94	5.90–5.97	6.18	6.15–6.21	5.93	5.91–5.94	6.00	5.95–6.05	6.21	6.16–6.29
	Alk	2.60	2.55–2.64	4.45	4.23–4.67	9.43	6.61–12.3	2.47	2.47–2.47	4.59	3.23–4.59	17.3	14.2–20.5
	DO	N/A		N/A		N/A		N/A		N/A		N/A	
1 April	pH	5.89	5.89–5.89	6.0	6.07–6.10	6.25	6.14–6.36	5.90	5.89–5.90	6.49	6.49–6.49	6.53	6.51–6.55
	Alk	2.53	2.52–2.53	9.59	7.71–11.5	12.9	9.31–16.4	2.64	2.55–2.72	22.4	22.1–22.8	25.9	25.1–26.7
	DO	5.50		1.60		4.40		11.2		1.20		1.20	
4 April	pH	5.85	5.84–5.86	6.32	6.31–6.32	6.26	6.26–6.26	5.87	5.86–5.88	6.15	6.04–6.24	6.31	6.12–6.15
	Alk	2.29	2.26–2.32	9.09	7.01–11.2	13.8	12.7–14.9	2.35	2.33–2.38	8.07	4.47–11.9	12.4	6.04–18.7
	DO	11.5	11.4–11.6	5.80	5.60–6.00	4.10	1.00–7.20	10.4	9.60–11.2	4.10	0.80–7.60	4.60	4.00–5.20
8 April	pH	5.96	5.96–5.96	6.19	6.16–6.21	5.93	5.90–5.96	5.94	5.94–5.94	6.18	6.18–6.19	6.44	6.42–6.47
	Alk	2.35	2.33–2.36	9.85	8.03–11.7	4.32	4.11–4.53	2.33	2.32–2.34	9.28	9.06–9.49	20.7	20.0–21.4
	DO	10.5	9.60–11.4	8.10	5.60–10.6	1.10	0.60–1.60	10.4	10.0–10.8	6.90	3.20–10.8	1.70	0.80–2.60
24 April	pH	6.14	6.13–6.14	5.90	5.85–5.94	6.26	6.16–6.36	6.10	6.09–6.11	6.35	6.10–6.59	6.36	6.29–6.49
	Alk	2.85	2.80–2.90	6.39	3.95–8.83	15.8	15.3–16.3	2.88	2.90–2.86	18.7	10.6–26.8	20.3	15.7–24.9
	DO	10.9	10.6–11.2	8.70	6.20–11.2	3.30	3.20–3.40	11.2	11.0–11.4	1.60	1.20–2.00	1.40	1.20–1.60
12 June	pH	6.39	6.39–6.40	6.20	6.15–6.25	6.05	6.00–6.0	6.48	6.48–6.49	6.38	6.29–6.46	6.51	6.45–6.58
	Alk	3.46	3.26–3.66	7.72	4.46–11.0	8.35	8.55–9.14	3.65	3.58–3.72	24.0	20.2–27.8	27.7	26.0–29.3
	DO	10.6		4.2		3.6		8.8		8.6		1.4	

zone. The mayflies most commonly encountered at the lower depth zones were leptophlebiids (*Leptophlebia cupida* Say, *Paraleptophlebia adoptiva* McD., and *Habrophlebia vibrans* Needham), although small ephemerellids (*Eurylophella verisimillis* McD. and *E. funeralis* McD.) were also found. All stonefly genera were found in the hyporheos at some point during the study period, but *Leuctra* was found most frequently and in the highest numbers. Trichoptera were not common in the hyporheic zone, although they were well represented at the surface. However, small net-spinning larvae (*Hydropsyche*, *Cheumatopsyche*, and *Chimarra*) were found in October and December to depths of 10–15 cm. Coleoptera, Megaloptera, and Odonata were rarely found in any depth zone.

Chemistry and hydrology

Discharge during the study period ranged from 5.6 to 878.5 L/s (Fig. 4). The peak flows in autumn (November) and late spring (May) were the result of rain storms, while the maximum flows in early spring (late March and April) were due to the combination of the melting of the surrounding snowpack and the ice from the lake. The pH of surface water ranged from a maximum of 6.7 in the summer to a minimum of 5.9 recorded during peak flows in spring ($\bar{x} \pm \text{SE} = 6.25 \pm 0.04$; $N = 42$). Alkalinity ranged from 2.43 to 4.18 mg $CaCO_3$/L ($\bar{x} = 3.26$) and dissolved oxygen varied from 6.8 to 12.9 mg/L ($\bar{x} = 9.9 \pm 0.17$, $N = 41$) during the study.

Spring Flood Patterns

Invertebrates

The pattern of invertebrate distribution varied between reaches during the flood. Total invertebrate abundance decreased sharply in surface samples in the riffle at the beginning of the flood and then remained relatively constant for the rest of the study period (Fig. 5a). The greatest reduction within this total was for blackfly larvae, while densities for other invertebrates were largely unchanged (Fig. 5b). In contrast, there was little change in surface density in the pool with the initial increae in discharge (Fig. 5a). However, by day 2 of the flood (24 h after onset of flooding), numbers in the pool reach (again primarily Simuliidae) increased in surface samples before gradually dropping to preflood levels by day 8 (Fig. 5a, 5b).

Hyporheic densities were extremely variable at all depths in the riffle and very low in the pool during this period (Fig. 5). Numbers decreased for all groups within the hyporheos in the riffle reach following the onset of flooding, but this trend was not significant (Student's t; $p > 0.05$). An increase in numbers at 10–15 cm depth on day 4 of the flood (Fig. 5) was primarily due to an increase in noninsect invertebrates at that depth (Fig. 5c). Ostracods, oligochaetes, and nematodes represented the majority of the invertebrates found in the substrate at this time. Few insects were found in the hyporheos during the flood in either reach, and most of those present were chironomids.

Chemistry and hydrology

The surface water chemistry differed markedly from that of interstitial water in Harp Outflow during the spring snowmelt flood (Table 1). Both pH and alkalinity decreased slightly in surface water but increased in the substrate, especially on the rising limb of the snowmelt hydrograph (see Fig. 4); fluctua-

tions in both parameters were noted on the falling limb. Alkalinity was always higher in the substrate than at the surface regardless of hydrologic regime. Dissolved oxygen followed no consistent pattern within the substrate, ranging from 1.0–10.0 mg/L, and was near saturation at the surface.

Discussion

Seasonal Pattern

We found stream invertebrates in the shallow substrates of Harp Outflow throughout the year, supporting Williams' (1984) contention that the hyporheic zone is an important universal habitat for benthos. However, the pattern of abundance in the different depth zones varied seasonally and was related to the timing of recruitment of the dominant insect taxa. Invertebrates found in the hyporheos were generally small in size, and most of the insects found below 5 cm depth were in early developmental stages (developmental stage was determined by wingpad development in hemimetabolous insects and size in holometabolous ones; D. J. Giberson, unpubl. data). Most of the insects had their major recruitment period in the fall or early summer (mayflies: D. J. Giberson, unpubl. data; all other insects: R. J. Hall, unpubl. data), and the highest numbers in all depth zones corresponded to these periods. Small insects have been previously reported to use the substrate as a "nursery" (Coleman and Hynes 1970; Williams and Hynes 1974; Godbout and Hynes 1982), although strong seasonal patterns were not noted (Hynes 1974; Bishop 1973). Williams (1984) suggested that eggs may fall into interstitial spaces after oviposition, then the larvae hatch and eventually move from the deep sediments to the surface as a result of increased demands for space and/or food. In Harp Outflow, we found small-stage larvae of many taxa in the substrate before encountering them in surface samples.

Harp Outflow showed a unique pattern of depth distribution, however, when compared with other studies of the hyporheos of streams. The majority of the total stream invertebrate fauna was generally reported at >5-cm sediment depths, even where substrates were as shallow as those in Harp Outflow (Coleman and Hynes 1970; Bishop 1973; Williams and Hynes 1974; Hynes 1974, Morris and Brooker 1979; Hynes et al. 1976). However, most of the invertebrates in Harp Outflow were found from 0 to 5 cm into the sediments. This pattern was largely due to one taxon, *Prosimulium*, a surface-dwelling filter-feeder commonly reported in great numbers in riffles below lakes (Cushing 1963; Wotton 1979; Bronmark and Malmqvist 1984). When *Prosimulium* was excluded from the analysis, the pattern of depth distribution was similar to that found in other studies, and the hyporheic fauna dominated the total fauna.

The composition of the hyporheic fauna was similar to other studies, even for studies outside of Ontario or Canada (Coleman and Hynes 1970; Bishop 1973; Williams and Hynes 1974; Hynes et al. 1976). For example, the taxa most common in the substrates in Harp Outflow (chironomids (Diptera), leptophlebiids and small ephemerellids (Ephemeroptera), and detritivorous stoneflies (Plecoptera)) were also the most abundant in substrates in the Speed River, Ontario (Coleman and Hynes 1970; Williams and Hynes 1974) and in streams in Wales (Hynes et al. 1976) and Malaysia (Bishop 1973). Williams (1984) has suggested that invertebrates that inhabit the hyporheic zone must possess certain characteristics, such as small size, tubular-shaped bodies, and/or hard protective shells that withstand crushing, which allow them to colonize the interstitial habitat. These characteristics are all shared by the taxa listed above and probably contribute to the worldwide pattern.

The presence of large numbers of early instar *Prosimulium* in the substrate in the late fall – early winter was unexpected. Blackflies are usually considered to be restricted to the surface because they feed by filtering food particles from the current (Hynes 1970). However, first instar *Prosimulium* are very small, possess no fans (for filtering), and feed primarily on very fine organic material (D. A. Craig, University of Alberta, pers. comm.) which is common in interstitial spaces (Williams 1984). A recent study of the hyporheos in northwestern Ontario also recorded *Prosimulium* larvae to considerable depths (>30 cm; Jeffrey et al. 1986).

Noninsect arthropods were more common within the substrate than at the surface throughout the year in Harp Outflow. These are often found in riffle benthos or drift samples and are usually considered to be accidental imports from lentic areas, although it has been suggested that some may inhabit the hyporheic zone (Shiozawa 1986; Williams 1984). Our study indicates that they are an important component of the hyporheic community.

Conclusions

Short-term pH depressions of as much as two units, with major effects of biota, occur regularly in the poorly buffered Canadian Shield streams of south-central Ontario (Jeffries et al. 1979; Hall et al. 1980; Hall et al. 1982; Hall and Likens 1984; Hall et al. 1988). These depressions are often associated with the rapid increases in stream discharge that accompany snowmelt and the spring rains or the fall rains and concomitant reduction in evapotranspiration. The present study was intended to characterize organism response to the physical effects of flooding in the stable substrates of a Canadian Shield outflow stream which is not acidified. Our intention was to provide baseline data that would be helpful in separating the responses of the invertebrate fauna to physical as opposed to chemical effects in more acidified systems.

No statistically significant discharge-related vertical movements were noted in Harp Outflow and invertebrate densities (excluding blackflies) remained relatively constant in surface samples in the riffle throughout the flood period. This constancy is in contrast with other studies, where spates have been reported to drastically reduce benthic fauna in streams (McClay 1968; Scullion and Sinton 1983; Reice 1984). Subsequent rapid recolonization after spates, probably via vertical migrations (Williams and Hynes 1974; Williams and Hynes 1976; Poole and Stewart 1976), have lead many workers to suggest that invertebrates actively move into the substrate during a flood. The lack of evidence for such movements during the spring flood in the present study probably relates to the stability of the Harp Outflow substrates. Surface substrate materials in Harp Outflow were large and underwent little movement during the flood. They probably provided sufficient refugia to keep large numbers of organisms from being dislodged or forced into the hyporheos.

No movement patterns were related to changes in the chemistry of the system. Harp Outflow is not considered to be affected by acidic precipitation and no effects were anticipated. However, flood conditions were related to some interesting patterns in the pH and alkalinity of the interstitial water. pH showed

no consistent trend with depth in the substrate at low flow, but was always higher in the substrate during the spring flood. Alkalinity was also higher in the substrate.

These results contrast with those reported from hardwater streams in which pH has been shown to decrease with depth in the substrate (Burbanck and Burbanck 1967; Williams and Hynes 1974; Williams 1984). The contrast in patterns is probably related to differences in groundwater chemistry (Bottomly et al. 1984; Reuss and Johnson 1985; Reynolds et al. 1986). During a flood, groundwater makes up the major portion of streamwater on the rising limb of the hydrograph (Hynes 1983; Bottomly et al. 1984). In hardwater, high-alkalinity systems characterized by thick soil overburdens, soil decomposition processes and concomitant production of CO_2 are expected to exert the major influence on shallow groundwater chemistry, decreasing the pH and alkalinity of water moving through the streambed. In softwater, lower-alkalinity systems with thin to nonexistent soil cover, generation of base cations dominates groundwater chemistry, leading to increases in pH and alkalinity. Our study shows the importance of taking pH and/or associated chemical measurements from the habitat actually occupied by stream invertebrates, since the pH of water even a few centimetres into the substrate can differ markedly from that of the water column.

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Appendix: List of Taxa

Insecta
- Ephemeroptera
  - *Leptophlebia*
  - *Paraleptophlebia*
  - *Habrophlebia*
  - *Baetis*
  - *Eurylophella*
  - *Stenonema*
  - *Isonychia*
- Plecoptera
  - *Isoperla*
  - *Malenka*

Podmosta gp.
Taeniopteryx
Leuctra
Odonata
Calopterygidae
Gomphidae
Megaloptera
Nigronia
Trichoptera
Cheumatopsyche
Hydropsyche
Chimarra
Rhyacophila
Ptilostomis
Diptera
Prosimulium
Simulium
Orthocladiinae
Tanypodinae
Chironomini
Tanytarsini
Tipulidae
Ceratopogonidae
Empididae
Coleoptera
Elmidae
Ectopria

Crustacea
Copepoda
Ostracoda
Cladocera

Mollusca
Pisidiidae

Nematoda

Annelida
Oligochaeta

Arachnida
Acarina

Apparent Digestibility in Rainbow Trout (*Salmo Gairdneri*): Influence of Hypoxia

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Pouliot, T., and J. de la Noüe. 1988. Apparent digestibility in rainbow trout (*Salmo gairdneri*): influence of hypoxia. Can. J. Fish. Aquat. Sci. 45: 2003–2009.

We assessed the influence of hypoxia, which is likely to reduce the productivity of fish culture, on the digestibility of nutrients in rainbow trout (*Salmo gairdneri*). Rainbow trout (seven to each diet) were kept for 8 d in water with an oxygen saturation level of 40.0 ± 4.0%, while control fish were kept in 89.4 ± 4.2% oxygen-saturated water. Three isonitrogenous and isocaloric diets composed of different sources of protein (animal, plant, and mixed) were used. The apparent digestibility coefficients (ADC) were calculated by the indirect method (chromic oxide) after the automatic collection of feces. The experimental hypoxia used did not change the ADC for protein (total nitrogen), gross energy, or dry matter. The amino acids only showed a tendency for better absorption: proline, glycine, alanine, and tryptophan had a significantly higher ADC ($P < 0.05$) in experimental fish than in control fish when the animal protein based diet was used. Finally, we noted that feed intake was diet dependent. In contrast with what we observed with the commercial (mixed protein sources) and plant protein based diets, the fish receiving the animal protein based diet maintained a normal (or returning to normal) feed intake when they were subjected to hypoxia.

L'hypoxie est un stress susceptible d'affecter la productivité dans un élevage piscicole. Dans le présent travail, l'influence de l'hypoxie sur la digestibilité des nutriments et la prise alimentaire de la Truite arc-en-ciel (*Salmo gairdneri*) est établie. Des truites arc-en-ciel (sept par régime alimentaire) sont gardées pendant huit jours dans une eau dont la saturation en oxygène est de 40,0 ± 4,0 %; les témoins reçoivent une eau saturée à 89,4 ± 4,2 %. Trois régimes alimentaires, isoprotéiques et isocaloriques, de qualité protéique variable (animale, végétale et mixte), sont utilisés. Les coefficients d'utilisation digestive apparente (CUDa) sont obtenus par la méthode indirecte (oxyde de chrome) après récolte automatique de fèces. Les résultats obtenus permettent de démontrer que l'hypoxie expérimentale utilisée n'affecte pas la digestibilité apparente des protéines (azote total), de l'énergie totale et de la matière sèche. Seuls les acides aminés ont tendance à être mieux absorbés : la proline, la glycine, l'alanine et le tryptophane ont un CUDa significativement plus élevé ($P < 0,05$) lorsqu'un régime à base de protéine animale est utilisé. Enfin, la prise alimentaire dépend du régime distribué aux truites. En effet, contrairement à ce qui se passe avec les régimes commercial et végétal, les truites alimentées avec un régime à base de protéines animales conservent une prise alimentaire normale (ou qui revient à la normale) lorsqu'elles sont soumises à l'hypoxie.

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The lowering of the oxygen content of water (hypoxia) is known to be an important stressor for fish (Fry 1969). Hypoxia exists when water oxygen saturation is below the accepted minimum of 60%. Intensive fish-farms which seek maximal biomass production are especially prone to experience this type of stress during summer; a reduced growth rate and even increased mortality may result, with obvious economic consequences.

Few studies have been published on the influence of stress on nutrient digestibility in fish. Neff and Mussachia (1967) noticed that anaerobiosis modified L-leucine active transport in *Stenotomus versicolor* and *Ictalurus nebulosus*. Under similar experimental conditions, Bogé et al. (1979) observed a reduction of glycine absorption in rainbow trout (*Salmo gairdneri*).

An in vitro technique essentially characterizes the cellular mechanisms of the intestinal absorption of nutrients, whereas the information gained in vivo bears on digestive functioning integrated with the whole physiological functions of the organisms. In *S. gairdneri*, the in vivo digestibility studies done with perfusion techniques have generally been devoted to intestinal absorption. These techniques require the use of catheters and immobilization of the fish which can be a source of stress in itself and may change absorption. The measurement of the apparent digestibility of nutrients (i.e. ingested quantity minus excreted quantity) may be a useful way for obtaining infor-

mation on the utilization of nutrients by trout under hypoxic stress.

Because the structure of proteins (fibrillary versus globular) may influence digestion efficiency, we found it interesting to compare the influence of hypoxia on the apparent digestibility of diets containing different proteins (animal versus plant). Our aim was to measure the apparent digestibility of crude protein, amino acids, gross energy, and dry matter in rainbow trout fed various diets based on animal or plant protein sources with and without hypoxic stress.

Materials and Methods

Rainbow trout weighing 120 ± 24 g were obtained from a local fish farm (Pisciculture des Alléghanys, St-Philémon (Qué.)). They were kept in 60-L tanks each supplied with 4 L water/min recirculated by passage through a biological filter. The photoperiod was 12 h light : 12 h dark and the water temperature was constant at 15 ± 0.5°C. The various parameters for water quality (NH_4^+, NO_2^-, NO_3^-, pH) were monitored and in each case did not exceed the recommended values for rainbow trout (MAPAQ 1982).

Three isonitrogenous and isocaloric diets were used (Table 1). These diets were formulated to satisfy the nutrient requirements for coldwater fish as defined by NRC (1981). One was a commercial diet; the other two were test diets where protein originated predominately from animal sources or exclusively from plant proteins. All diets were stored at −20°C until required for feeding.

The fish were individually weighed, marked, and separated into three groups each given a different diet. The fish were fed their respective diets for 149 d (November to January). The total daily ration was 1.5% of live weight and was manually distributed twice a day, i.e. at 0800 (2h after lights were turned on) and at 1600 (2h before lights out). Following this adaptation period, fish were again individually weighed and the growth rate for each diet was calculated and compared (Table 2).

After adaptation, groups of seven fish for each diet were subjected to hypoxic conditions for 8 d. In parallel, a group of seven fish was used as a control for each of the three diets. This protocol was repeated three times on three separate groups (feed intake being measured twice). Time for the fish to acclimate to the hypoxic conditions was not provided, since we wished to measure any changes in digestibility from the onset of hypoxia.

Water oxygen concentrations were measured with an YSI oxymeter (model 58) and were controlled with a deoxygenation chamber as described by Mount (1961, 1964). The control tanks received water with an oxygen saturation level of 96.0 ± 3.0%, while the experimental tanks were 59.0 ± 3.0% saturated. Following addition of the fish to each tank the actual oxygen saturation levels were 89.4 ± 4.2 and 40.0 ± 4.0% for water in the control and experimental tanks, respectively.

TABLE 1. Composition of diets (% dry wt. basis).

		Diet		
Feed composition	Protein level	Commercial	Animal based	Plant based
Wheat middlings	15.0	31.500	34.500	
Corn gluten meal	60.0	9.000		18.000
Poultry by-product meal	58.0	5.000	28.000	
Brewer's yeast	44.6	5.000		
Feather meal	81.5	5.000	12.000	
Herring meal	70.0	25.000		
Soybean meal	48.0	10.000		65.000
Blood meal[a]	85.0		11.500	
Herring oil[b]		7.000	10.200	11.100
Calcium phosphate		1.000	1.500	3.200
Sodium chloride		0.300	0.300	0.300
Endox 50		0.025	0.025	0.025
Choline		0.846	0.630	0.868
Vitamin premix[c]		0.250	0.250	0.250
Mineral premix[d]		0.100	0.100	0.100
Calcium carbonate				0.700
Lysine			0.640	0.300
Methionine			0.330	0.240
Total		100.000	100.000	100.080
Crude protein[e]		44.6±0.5	43.8±0.7	44.6±0.3
Lipids[e]		12.1±0.1	16.1±0.1	12.9±0.4
Energy (kJ/g)[e]		19.0±1.2	20.3±1.8	21.0±2.1
Ash[e]		7.7±0.1	7.2±0.2	7.5±0.1
Moisture[e]		7.0±0.1	7.3±0.2	6.6±0.6

[a]Processing method: steam jacket.

[b]Stabilized by ethoxiquin.

[c]The vitamin supplements supplied the following nutrients (IU/kg or mg/kg of diet): A, 3332 IU; D_3, 2082 IU; E, 75 IU; K, 17.7; B_{12}, 0.25; riboflavin, 16.8; pantothenic acid, 52.3; niacin, 167; folic acid, 8.3; thiamine, 16.7; pyridoxine, 12.5; biotin, 0.165; ascorbic acid, 333.0.

[d]The mineral supplement supplied the following nutrients (mg/kg of diet): manganese, 43; zinc, 72; iodine, 4; iron, 31.5; copper, 12.4.

[e]Mean values ± standard deviation (n = 3).

TABLE 2. Weight of trout before and after 149 d of feeding on the experimental diets.

Diet	N	Inital mean weight (g)[a]	Final mean weight (g)	Growth rate (%/day)[b]	Condition index (weight/length³)
Commercial	28	134 ± 30	378 ± 86	0.68 ± 0.15	124 ± 0.15
Animal based	29	162 ± 31	396 ± 69	0.55 ± 0.13[c]	1.27 ± 0.14
Plant based	25	150 ± 31	369 ± 86	0.59 ± 0.15[d]	1.27 ± 0.10

[a]Mean values ± standard deviation.
[b]$\ln W_2 - \ln W_1/T_2 - T_1$ (Ricker 1979).
[c]Statistical significance ($P<0.005$) between animal-based and commercial diets.
[d]Statistical significance ($P<0.025$) between plant-based and commercial diets.

The measurement of the apparent digestibility coefficients (ADC) was conducted by the indirect method using chromic oxide as an inert marker in the diets. Feces were collected over 24-h periods throughout the 8-d period, using the automatic fish feces collector of Choubert et al. (1981) which allows recovery of feces between 6 and 15 s after emission. These were frozen at −40°C until analyzed. It was possible to separate noningested food matter from the feces; therefore, daily feed intake could be easily quantified for each of three replicates. Data are presented in percent of feed intake where 100% indicates a complete feed of the daily ration.

The analyses of feces and diets for crude protein (Automatic Kjel-Foss), gross energy (Phillipson micro-bomb), chromium (Arthur 1970), amino acids (Beckman Autoanalyzer 6300), and lipids (Goldfish extraction apparatus) were carried out on lyophilized samples. Dry matter was measured by heating at 92°C for 24 h until a constant weight was obtained. The ADCs were calculated according to the equation of Maynard and Loosli (1969) and were expressed as percentages.

Statistical Analysis

The experimental design used was a fully random block (Steel and Torrie 1960). The Waller–Duncan test with $\alpha = 0.05$ was used to compare the ADC averages (protein, energy, dry matter, and amino acids) in relation to the degree of water oxygenation (normoxic or hypoxic) and the experimental period (days). This comparison was done for each diet provided that the variance ratio (F-test of variance analysis) was significant (Snedecor and Cochran 1957). When the ADCs were not significantly influenced by the hypoxic stress but were showing a general tendency, the nonparametric method of the sign test (Snedecor and Cochran 1957) was used to verify whether this general tendency of ADCs to increase or decrease was significant or not.

Results

Oxygen Conditions

Despite the stability of oxygen conditions during most of the light period (Fig. 1), some short and intermittent decreases occurred when the lights were switched on, and at meal times. After lights out, the water oxygen content rose gradually in the control and experimental tanks until the lights were switched on again.

Feed Intake

Nearly all the feed distributed was ingested by the control fish (normoxic conditions) but hypoxia generally resulted in decreased feed intake (Fig. 2). However, the fish fed the animal protein based diet (Fig. 2c) behaved differently from the fish fed the other two diets (Fig. 2a, 2b), i.e. during the first replicate, the former did not show reduced food intake due to hypoxia whereas during the second replicate, food intake declined initially and then returned to normal after 5 d.

Digestibility Studies

For a given diet and a given oxygenation condition (Fig. 3a) the protein ADC was constant for the entire experimental period for all diets ($P > 0.05$) and the two oxygenation conditions ($P > 0.05$). Whatever the diet, there was no difference between the ADCs of the normoxic and hypoxic animals. However, the average ADCs for protein of the plant protein based diet (92.2 ± 2.6%), the commercial diet (88.0 ± 2.9%), and the animal protein based diet (78.9 ± 5.2%) were all significantly different ($P < 0.05$).

Because hypoxia did not lead to any ADC change, whatever the diet given the fish, the significant differences ($P < 0.05$) found for the ADC of gross energy pertained only to the diets (Fig. 3b). The plant protein based diet was the most digestible (79.1 ± 3.3%) followed by the commercial diet (76.1 ± 3.5%) and the animal protein based diet (72.7 ± 3.7%).

For dry matter ADC, also, the only significant difference was found among the diets (Fig. 3c). The ADCs of the dry matter of the plant protein based and commercial diets were the same (68.6 ± 3.4 vs. 67.8 ± 3.9%, respectively) but was higher than for animal protein based diet dry matter (61.8 ± 4.5%) ($P < 0.05$).

The plant protein based diet (Fig. 4) showed an average ADC of amino acids of 91.1 ± 8.6% with a coefficient of variation of only 3%. The general decrease in ADC due to hypoxia was significant ($P < 0.05$) only with the sign test. The average ADC for amino acids of the commercial diet was 85.5 ± 5.1% (coefficient of variation of 6%), and again only the sign test showed a general and significant ($P < 0.05$) increase of amino acid ADC caused by hypoxia. Fish adapted to the animal protein based diet showed a lower amino acid ADC (average of 75.8 ± 1.1%) than fish receiving the other diets. Moreover, the coefficient of variation was 15%, indicating a higher variation of ADC from one amino acid to the other for fish fed the animal protein based diet than for the other two diets. For the animal diet there was a general increase of amino acid ADC ($P < 0.05$, sign test) due to hypoxia and this increase was also significant ($P < 0.05$, Waller–Duncan) for some individual amino acids such as tryptophan, proline, glycine, and alanine.

Fish Growth

The various groups of fish did not differ significantly ($P > 0.05$) with respect to condition index and average final weight

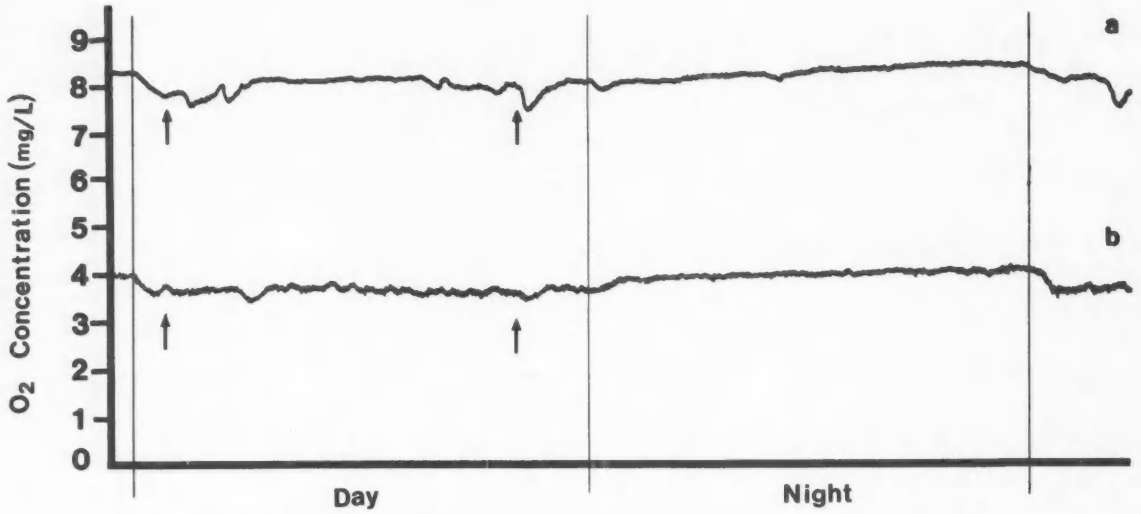

FIG. 1. Oxygen concentration in tanks at 15°C under (a) normoxic and (b) hypoxic conditions. Arrows indicate meals.

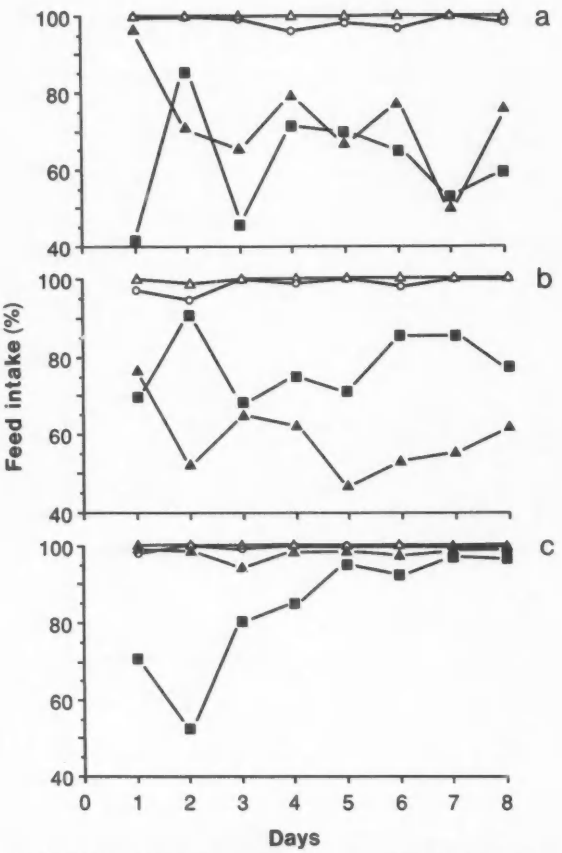

FIG. 2. Dietary intake of trout fed (a) commercial, (b) plant protein based, and (c) animal protein based diets under normoxic (△, ○) and hypoxic (■, ▲) conditions.

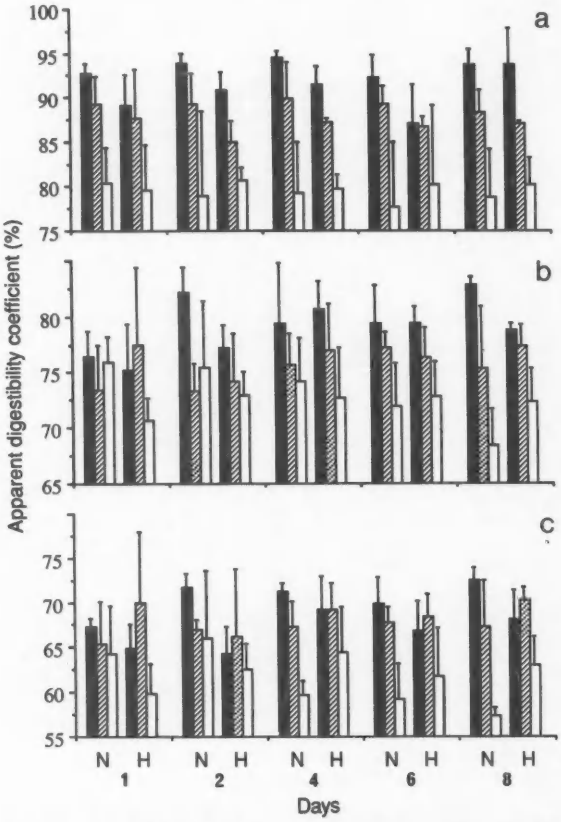

FIG. 3. Apparent digestibility coefficient (ADC) (mean ± SD, N = 3) of (a) crude protein, (b) gross energy, and (c) dry matter for fish fed plant protein based (■), commercial (▨), and animal protein based (□) diets under normoxic (N) and hypoxic (H) conditions.

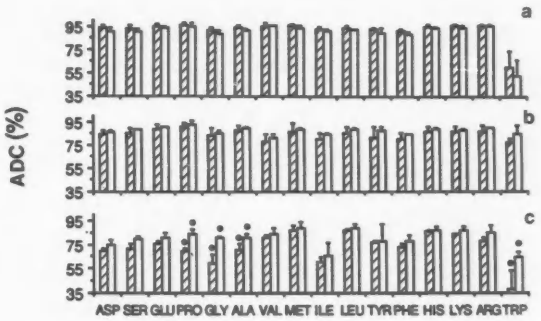

FIG. 4. Apparent digestibility coefficient (ADC) (mean ± SD, N = 3) of amino acids for fish fed (a) plant protein based, (b) commercial, and (c) animal protein based diets under normoxic (▨) and hypoxic (□) conditions. Statistical significance ($P < 0.05$) between normoxic and hypoxic conditions.

after 149 d of feeding the three diets (Table 2). However, growth rates were significantly different between the commercial and animal diets ($P \leq 0.005$) and between the commercial and vegetal diets ($P \leq 0.025$). The best growth was obtained with the commercial diet.

Discussion

Water Oxygenation Conditions

For the present study we needed a supply of water with a precisely regulated oxygen concentration held constant for an extended period of time. This condition was satisfied (Fig. 1). The periodical and transient variations in oxygen concentration during the photoperiod stemmed from the fact that rainbow trout display nocturnal feeding behaviour, with intensive swimming activity at dawn and at dusk (Landless 1976). The small variations observed in oxygen concentration were probably due to the increased physical activity of fish and to the starting digestion of food, which is correlated with an increased oxygen consumption (Staples and Nomura 1976).

Feed Intake and Hypoxia

Despite the variability in daily feed intake, no significant modification of apparent digestibility of nutrients due to hypoxia was observed. It is known that an increase in the food intake of rainbow trout is correlated with a decreased ADC (Elliot 1976; Wurtsbaugh and Davis 1977; Windell et al. 1978; Hudon 1985). Therefore, we might expect that a decrease in feed intake would lead to increased ADCs. Such a relationship would, however, call for a control mechanism at the level of digestive enzyme activity. McLeese and Stevens (1982) demonstrated that such a control mechanism does not exist in rainbow trout, at least not for trypsin and chymotrypsin. Moreover, Windell et al. (1978) indicated that ADCs stabilize when feed intake is below a given threshold. Huisman (1976) observed that the efficacy of dietary energy utilization in rainbow trout expressed as a function of the weekly quantity of food dispensed in (kilocalories per kilogram)$^{0.8}$ live weight increases up to a ration of 212 kcal/kg$^{0.8}$ (886 kJ/kg$^{0.8}$). A plateau is then reached from 200 to 350 kcal/kg$^{0.8}$ (836–1463 kJ/kg$^{0.8}$) and then there is a gradual decrease. For the experimental conditions we used for the digestibility studies, the energy intake varied from 286 to 406 kcal/kg$^{0.8}$ (1199–1701 kJ/kg$^{0.8}$) per week. The energy intake was therefore maintained within the limits of the model described by Huisman (1976). Thus, even if feed intake was reduced by half, the ADC values would be anticipated to be stable.

Fish experiencing hypoxia had a lower feed intake than the control fish. However, fish fed the animal protein based diet maintained a normal feeding behaviour, or one which returned to normal, in contrast with what we observed for fish fed the other two diets. Food intake can be modified by the diet itself, since the amino acid profile of the diet influences the synthesis of neurotransmitters (Growdon 1979). For instance, the availability of plasma tryptophan and tyrosine can modify the synthesis of serotonin and catecholamines in the central nervous system (Fernstrom and Wurtman 1971a, 1971b; Carlsson 1974; Wurtman et al. 1974; Gibson and Wurtman 1977; Sved 1983). In fish, these monoamines are involved in the control of various physiological functions such as motor activity (Fenwick 1970; Fingerman 1976), behavioural thermoregulation (Byrne 1970; Fryer and Ogilvie 1978), or aggression (McIntyre et al. 1979). Some influence of diet composition on feeding behaviour therefore appears possible.

The measurement of biogenic amines in the central nervous system of trout under the same experimental conditions as in the present study indicated that the origin of the dietary protein (animal or plant) influenced the concentration of amines in the various brain structures (Pouliot et al. 1987). Moreover, hypoxia influenced amine concentration except in the hypothalamus of the trout fed the animal protein based diet. We know that this latter brain structure controls the activation of the endocrine system and especially feed intake. The fact that serotonin and catecholamine concentrations in the hypothalamus were not modified by hypoxia in the case of fish fed the animal protein based diet might explain why these fish generally had normal food ingestion.

Feed Intake, Digestibility, and Growth

The apparent digestibility of crude protein, amino acids, gross energy, and dry matter varied according to the diet; fish fed the animal protein based diet had the lowest ADC values in each case. The major ingredients in this diet (Table 2) were blood meal, feather meal, and poultry by-products meal. Cho et al. (1982, 1985) have shown that the apparent digestibility of these ingredients is rather low compared with that of ingredients from vegetal or marine origin. The presence of a poorly assimilated nitrogen source, such as keratin in feather meal, reduces the apparent digestibility. Thus, the significantly lower ADC ($P < 0.05$) found for dry matter of the animal diet compared with that of the two other diets fits with the data of Cho et al. (1982, 1985).

Fish meal is required to maintain optimum growth (Hilton and Slinger 1981). Replacing this protein source with vegetal protein or with various animal by-products would be expected to yield possibly poorer growth. This was the case with both our animal protein based and plant protein based diets. A greater difference between growth rates of fish fed the commercial diet and those fed the two other diets could have been obtained if the total daily ration had been ad libitum or 1.9%/d as recommended by Hilton and Slinger (1981) for this size fish.

Feed Intake, Hypoxia, and Digestibility

The apparent digestibility of crude protein, gross energy, and dry matter was not modified when rainbow trout were held in

a 60% oxygen-saturated water. However, one cannot rule out that more severe hypoxia than that in this study could have caused important modifications in digestion. In fact, anaerobiosis has been reported to impair in vitro intestinal amino acid absorption in trout (Bogé 1979).

It could also be that physiological adaptation processes to hypoxia did play a role in the response to such a stress. It is known that hypoxia leads to an increase in haemoglobin affinity to oxygen (Wood and Johansen 1972; Soivio et al. 1980; Tetens and Lykkeboe 1981; Nikinmaa and Soivio 1982; Bushnell et al. 1984). Because of this adaptation, the total quantity of oxygen in blood is only slightly lower than in normoxic conditions (Nikinmaa and Soivio 1982). Since we did not measure blood oxygen concentration, we lack the proper evidence for this proposition.

Hypoxia caused significant increases in the ADCs for proline, glycine, alanine, and tryptophan in trout fed the animal protein based diet. All these amino acids are involved in the energy metabolism of tissues. In trout, alanine and glycine play a role in gluconeogenesis (Walton and Cowey 1982) whereas proline is a glucoforming amino acid in higher vertebrates and in marine invertebrates (Fair and Sick 1982). Tryptophan is the precursor of nicotinamide adenine dinucleotide (NAD). Without NAD, glycolysis cannot proceed and the anaerobic synthesis of adenosine 5′-triphosphate (ATP) stops; hence, there is a reduced muscular output. Sor Medale (1985) noticed that hypoxia in rainbow trout lowers the plasma concentrations of proline, glycine, and alanine. Hence, there is a higher utilization of these amino acids in the tissues.

It is possible that the higher ADC of these amino acids is due to activation of Na^+,K^+-ATPase by glucocorticoids (Field 1978; Andrés et al. 1984) which are liberated during stress. In fish, as in mammals, the intestinal amino acid absorption is sodium dependent (Mepham and Smith 1966; Ward 1967). Na^+,K^+-ATPase that controls the sodium concentration in the intestinal tract is activated by glucocorticoids (Charney et al. 1975). Andrés et al. (1984) demonstrated that the subcutaneous injection of cortisol leads to an increase in the intestinal transfer of glycine and proline in hamsters.

During hypoxia, the freed corticoids may have stimulated Na^+,K^+-ATPase activity, leading to an overall increase of amino acid ADC for fish fed the commercial and animal protein based diets. Such an effect was not observed in fish fed the plant protein based diet. The amino acid ADC was high for fish fed this diet, i.e. 91% on the average (95% when tryptophan is excluded), so it could well be that the apparent digestibility of amino acids is already at its maximum. It should be mentioned that the absorption of amino acids in fish is a saturable phenomenon that obeys the Michaelis–Menten equation (Bogé et al. 1979; Cartier et al. 1979).

In conclusion, our findings suggest that the extent of experimental hypoxia used in the study did not affect the apparent digestibility of crude protein, gross energy, and dry matter. However, some amino acids appeared to have been better absorbed than others. Moreover, hypoxia appears to affect the feeding behaviour of rainbow trout and this depends upon the origin of the dietary protein.

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Particulate Organic Matter Export from Three Headwater Streams: Discrete versus Continuous Measurements

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Particulate organic matter (POM) export from three small headwater streams of the southern Appalachian Mountains was estimated using continuous and discrete (grab) measurement methods for 2 yr. Total annual POM export estimated from continuous measurements was always greater (28–68 kg ash-free dry mass (AFDM)) than estimates (8–44 kg AFDM) made from discrete measurements (i.e. POM concentration × total discharge). Continuous export samples were collected using a weir and gaging flume connected to a Coshocton proportional sampler designed to deliver 0.6% of discharge into a series of three settling barrels. The settling barrels removed a consistent proportion of POM (85–87%). The proportion of stream flow sampled by the Coshocton samplers was constant for each of the samplers (range 0.53–0.6%). The constant extraction efficiencies and proportional sampling of discharge allowed for the calculation of total export independent of discharge measurements (i.e. total export = amount in barrels ÷ extraction efficiency ÷ Coshocton percentage). The inability of the discrete method to adequately sample storm and bedload transport accounts for the underestimates of total annual export. This underestimation has important implications for studies which use discrete measurements to estimate POM export.

La quantité de matières organiques particulaires (MOP) rejetées par trois petits cours d'eau d'amont de la partie sud des Appalaches a été estimée pendant deux ans à l'aide de méthodes de mesures continues et discrètes (aléatoires). La quantité annuelle totale de MOP éliminées estimée par mesure continue était toujours plus grande (28–68 kg de matière sèche sans cendre (MSSC)) que celle estimée (8–44 kg (MSSC)) par les mesures discrètes (c.-à-d. concentration de MOP × débit total). Les échantillons de mesure en continu ont été prélevés à l'aide d'un déversoir et d'un canal de jaugeage relié à un échantillonneur proportionnel Coshocton conçu pour diriger 0,6 % de l'écoulement dans une série de trois barils de décantation. Ces barils retenaient une proportion constante des MOP (85–87 %). La proportion de l'écoulement prélevé par les échantillonneurs Coshocton était constante pour chacun des échantillonneurs (gamme : 0,53–0,6 %). L'efficacité d'extraction constante et le prélèvement proportionnel du débit ont permis de calculer les rejets totaux indépendamment des mesures de débit (c.-à-d. rejets totaux = quantité dans les barils + efficacité d'extraction + % de Coschocton). L'incapacité de la méthode discrète à échantillonner adéquatement les transports de crues et de fond explique la sous-estimation de la quantité annuelle totale. Cette sous-estimation a d'importantes incidences sur les études où l'on fait appel à des mesures discrètes pour estimer les MOP éliminées.

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Unidirectional downstream transport is an important element in conceptualizing streams as longitudinally linked systems (Vannote et al. 1980; Minshall et al. 1985) or as net importers or exporters (Cummins 1974) of energy, nutrients, or organic matter. Therefore, considerable attention has been placed on measuring and characterizing export, concentration, and composition of stream seston. The majority of export measurements have been made in streams draining cool temperate forests of North America and Europe and have utilized noncontinuous measurements of export (i.e. discrete grab samples) weighted on the basis of discharge (Fisher and Likens 1973; Hobbie and Likens 1973; Bormann et al. 1969) or time (Brinson 1976; Naiman 1976). Malmqvist et al. (1978) is one of the few studies whch have made continuous measurements over an extended period of time, although their estimates are still dependent on discharge measurements.

The errors associated with export measurements have been considered as problems associated with laboratory methods (i.e. filter weights, ashing techniques, and carbon determinations) or with replicability of the grab seston estimate (Baker et al. 1974; Perry and Rose 1984; Hickel 1984) rather than as problems associated with the type of sample collected. The objectives of this study were to compare discontinuous measurements weighted for discharge with continuous measurements of export and to examine the factors which are responsible for differences between the two methods.

Study Sites

Three small headwater streams, located at the U.S. Forest Service Coweeta Hydrologic Laboratory (CHL), Macon

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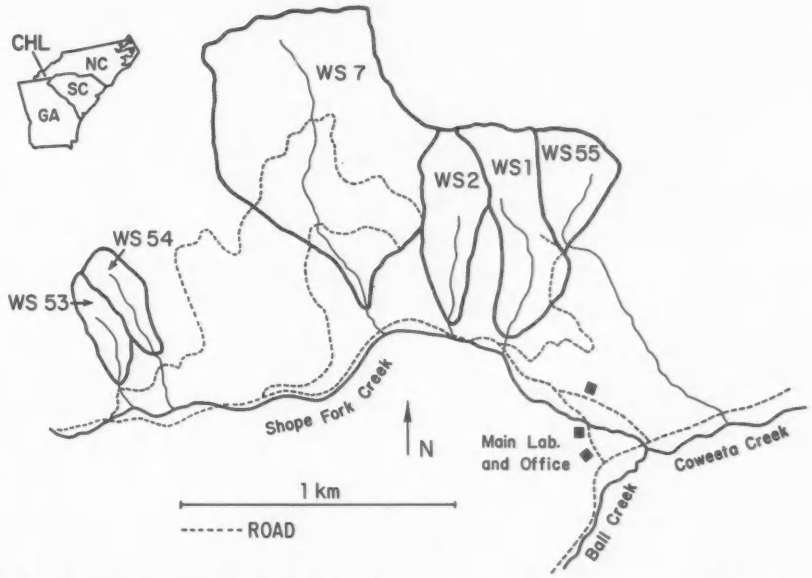

FIG. 1. Location of the Coweeta Hydrologic Laboratory (CHL), the three study streams draining catchments 53, 54, and 55, and the stream (WS 2) used to estimate winter discharges.

TABLE 1. Characteristics of study streams. Elevations were measured at the gaging flumes. Discharges are for the period January 1985 – March 1987.

	WS 53	WS 54	WS 55
Catchment			
Area (ha)	5.2	5.5	7.5
Elevation (m asl)	829	841	810
Channel			
Length (m)	135	260	170
Bankfull area (m^2)	365	406	314
Gradient ($cm \cdot m^{-1}$)	27	33	20
Discharge ($L \cdot s^{-1}$)			
Average	0.53	0.81	0.93
Maximum	22.87	22.76	24.07
Minimum	0.06	0.05	<0.01
Temperature (°C)			
Average	12.9	12.4	12.7
Maximum	19.5	19.5	19.4
Minimum	1.5	3.3	1.6
Annual degree-days	4696	4541	4626

County, North Carolina, USA (Fig. 1), were chosen for study. These streams are located in the Blue Ridge Province of the southern Appalachian Mountains. All three streams are first order, have southern aspects, and are heavily shaded by mixed hardwood forests and riparian rhododendrons. They are high-gradient streams with similar elevations, stream areas, thermal regimes, and discharge patterns (Table 1). Stream substrates consist of either rock outcrops (15–30% of channel area) or areas of cobble and boulders intermixed with sand and gravel. These streams are similar to other streams at CHL in being characterized by low ion concentrations (<1 mg·L^{-1}) and pH of 6.6–6.8 (Swank and Douglass 1975). There have been few disturbances in the study watersheds since the 1930's. WS 53 was experimentally treated with methoxychlor in 1980 (Cuffney et al. 1984; Wallace et al. 1982b). In 1961–62 the entire Coweeta basin was sprayed with DDT to control the elm spanworm (*Ennomos subsignarius* (Hubner)) (Grzenda et al. 1964). Additional site descriptions for WS 53 and WS 54 can be found in Wallace et al. (1982b, 1986a, 1986b) and Cuffney et al. (1984).

Materials and Methods

Continuous Export Estimates

A 2-ft-diameter (0.6m) Coshocton wheel proportional runoff sampler (Parsons 1954) mounted below a portable weir (Fig. 2) was used to deliver 0.6% of stream flow into three covered 125-L settling barrels. Water entered near the bottom of each barrel and exited just below the surface. This arrangement maximized settling and minimized the loss of floating particles. A hardware cloth trap (mesh = 4 × 4 mm) placed upstream of the weir excluded large particulate organic matter (POM) and prevented clogging of the flume or Coshocton wheel sampler. The collection apparatus was sampled at weekly (10 December 1984 – 14 May 1985) or biweekly (14 May 19 85 – 7 December 1986) intervals over a 2-yr period. Export data from WS 54 after December 1985 are not reported here because this stream was used in an experimental manipulation.

Export barrels were sampled by first flushing out the pipe leading from the Coshocton sampler to barrel 1 by holding the opening of the Coshocton sampler in the outflow of the weir for 15–30 s. Average water depth in each barrel was estimated from four measurements evenly spaced around the circumference of the barrel. Water volume in the barrel was then calculated from a regression relating water depth (centimetres) and volume (litres) (i.e. volume = 1.6663 ×

depth − 3.0829; r^2 = 0.999). Concentrations of particles in each barrel were measured by vigorously stirring the water and then collecting three replicate aliquots at about middepth near the middle of the barrel. Each aliquot was filtered through a preweighed and ashed glass fiber filter (Gelman type A/E). The amount of water filtered was varied with the amount of suspended material in each barrel. The amount (grams ash-free dry mass (AFDM)) of POM in each barrel (B) was calculated as

$$B = C \times [V_b \div V_f]$$

where C is the POM concentration (grams AFDM per litre) and V_b and V_f are the volume (litres) of water in the barrel and the aliquot filtered. Total amount in the barrels (B_t) is the sum of the averages of the replicates for the three barrels.

Total export (Expt) in each collection interval was calculated as

$$\text{Expt} = B_t \div E_f \div C_s$$

where E_f is the export barrel extraction efficiency, B_t is the amount (grams AFDM) recovered from the three barrels, and C_s is the proportion of discharge sampled by the Coshocton subsampler. Export barrel extraction efficiencies (i.e. [inlet concentration − outlet concentration] ÷ inlet concentration) and proportion of total flow sampled by the Coshocton sampler (i.e. inlet discharge ÷ flume discharge) were measured during the period of weekly samplings.

The H-flumes acted as sediment traps and required periodic cleaning to maintain accurate stage measurements. Cleanings were done approximately once a month after all barrels had been sampled and emptied. Flumes were cleaned by slowly resuspending the material in the flume while the Coshocton subsampler was filling barrel 1. Flume cleanings lasted 5–30 min depending on the amount of material in the flume. After the flume was cleaned, barrel 1 was sampled as described above. Organic matter contained in the flume was calculated as amount in barrel 1 ÷ Coshocton percentage. The amount of POM recovered from the flume was usually apportioned over two sampling periods in relation to the amount of POM exported in each sampling period (i.e. amount in flume × amount in export collection period 1 ÷ total export in periods 1 and 2).

Grab Export Estimates

Grab export samples were taken immediately prior to collecting barrel samples. Grab samples were collected at the mouth of the gaging flume after the Coshocton subsampler was stopped. Extreme care was taken to avoid disturbing the flume or stream while collecting grab samples. Sample volumes were determined by the amount of material in export and ranged from 2 to 8 L. Six grab samples were taken from each stream on each sample date and filtered through preweighed and ashed glass fiber filters (Gelman type A/E). Export was calculated as average concentration × total discharge during the sampling interval. Average concentration was the mean of the POM concentrations measured at the beginning and end of the sampling interval. Filters from grab, barrel, and flume cleanings were dried (60°C for 5 d), weighed, ashed (500°C for 1–2 h), rewetted, dried (2 d), and reweighed to determine ash content and AFDM.

Discharge

Stream flow at the base of each watershed (Fig. 1) was channeled into a 1.5-m-long plywood trough with a 1-ft (0.3 m) H-flume (Agricultural Research Service 1962) attached to the downstream end (Fig. 2). Stage heights were continuously measured during nonfreezing months (i.e. April – November) using a strip chart recorder at a stilling well connected to the H-flume (Fig. 2). Discharge rating curves (i.e. stage in centimetres versus discharge in litres per second) were derived for each watershed from field measurements and used to calculate instantaneous and total daily discharges from stage data. WS 2 (Fig. 1) discharge (i.e. daily average, maximum, and minimum) was used to estimate study stream discharge during ungaged months (December – March). These discharge estimates were based on regression equations developed during gaged months.

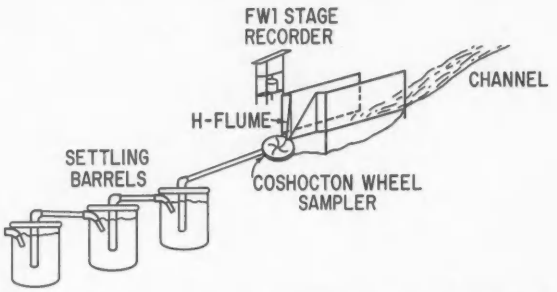

FIG. 2. Sampling apparatus used to collect continuous data on seston export. The Coshocton wheel proportional sampler transfers ~0.6% of the stream flow into the three covered 100-L settling barrels. Water enters each barrel at a point ~45 cm below the water surface (~15 cm above the bottom of the barrel). Water exiting the barrels is removed at ~10 cm below the water surface. The H-flume and FW1 stage recorder provide continuous discharge records during nonfreezing months (April–November).

TABLE 2. Seston barrel extraction efficiencies and percentage of stream flow sampled by Coshocton proportional samplers. Extraction efficiencies are calculated as (inlet concentration − outlet concentration) ÷ inlet concentration. Discharge range is the range of discharges over which extraction efficiencies were calculated.

	WS 53	WS 54	WS 55
Seston barrel extraction efficiencies			
Mean	0.8452	0.8704	0.8584
SE	0.0131	0.0120	0.0167
N	13	16	15
Coshocton flow subsample			
Mean	0.5988	0.6190	0.5339
SE	0.0091	0.0088	0.0073
N	20	20	21
Discharge range ($L \cdot s^{-1}$)	0.3–4.2	0.5–4.9	0.4–9.0

Results

Characteristics of Continuous Export Samplers

Field measurements indicated that the Coshocton proportional subsamplers sampled a very constant proportion of stream flow over a wide range of velocities (Table 2). However, the proportion of stream flow sampled differed

TABLE 3. Discharge ($L \cdot s^{-1}$) and residence time (h) in seston barrels during the two study years. Sample collection began on 10 December 1984 (i.e. year 1: 1984–85) and ended on 7 December 1986 (i.e. year 2: 1985–86). Percentiles (50th and 95th) refer to discharges below which 50 and 95% of the observations lie. Average, 50, and 95 percentile discharges are determined from data on mean daily discharges. Maximum and minimum discharges are determined from instantaneous discharges. WS 54 was experimentally manipulated during year 2 and data from that year are not included here.

	WS 53		WS 54	WS 55	
	Year 1	Year 2	Year 1	Year 1	Year 2
Discharge characteristics					
Average	0.58	0.33	0.91	0.94	0.50
50th	0.50	0.29	0.75	0.74	0.47
95th	1.25	0.63	1.94	2.29	1.06
Max.	13.91	22.87	12.95	13.97	24.07
Min.	0.16	0.14	0.25	0.15	0.05
Seston barrel residence times					
Average	23.9	42.1	15.3	14.8	27.8
50th	27.8	47.9	18.5	18.8	29.6
95th	11.1	22.1	7.2	6.1	13.1
Min.	1.0	0.6	1.1	1.0	0.6
Max.	86.8	99.2	55.6	92.6	277.8

significantly among the three Coshocton subsamplers. The Coshocton on WS 55 sampled significantly less flow than did those on WS 53 and WS 54 ($P < 0.05$, ANOVA, Student–Newman–Keuls test; Zar 1974). In addition, Coshocton samplers on WS 54 and WS 55 differed significantly from the expected (Parsons 1954) value of 0.6% (*t*-test; Zar 1974). These differences arise from variability in the construction, installation, and settling of the samplers.

Seston barrel extraction efficiencies were constant over the range of velocities reported in Table 2 and did not differ significantly among the three streams ($P < 0.05$, ANOVA; Zar 1974). The three seston barrels removed an average of 85.8% of the organic particles in transport. However, barrel extraction efficiencies were not measured during storms or at discharges >9 $L \cdot s^{-1}$; consequently the particle retention in the barrels at extreme discharges is not known empirically.

The design of the barrels limits the loss of floating particles but the deposition of nonfloating particles is a function of particle size and residence time. High discharges could reduce barrel extraction efficiencies by decreasing residence times, resulting in underestimates of export. Alternatively, efficiencies might increase if median particle size increases during storms (Wallace et al. 1982a), resulting in overestimates of export. Nevertheless, residence time in the barrels was seldom (i.e. <5% of the time) <6 h (Table 3), and even during maximum recorded discharge (23 $L \cdot s^{-1}$), residence time was 36 min and current velocities were sufficiently low (<0.14 $cm \cdot s^{-1}$) that extraction efficiencies of 78–86% would be expected (i.e. settling of particles >19 μm in diameter; T. F. Cuffney, unpubl. data; Morisawa 1968). In addition, most of the total organic matter retained by the export barrels (i.e. 82–92%, CV = 9%) settled out in the first barrel (Table 4). The amount recovered from barrel 3 was always <17%. Based on these calculations, the seston barrel efficiencies would not radically change over the entire range of discharge encountered.

Comparison of Grab and Continuous Export

The discrete (grab) method underestimated annual POM export obtained using the continuous method (Table 5) for all three streams and in both years. For the discrete method, underestimates developed immediately, continued to acrue through time (Fig. 3A), and were greatest for WS 53 (55–73%) and least for WS 55 (27–53%). Underestimates were greater during year 2 (10 December 85 – 10 December 86) than year 1. The amount of POM export that originated from H-flume cleanings was <10% of that collected by the seston barrels.

The differences between grab and continuous export estimates are primarily due to the inclusion of storms in the continuous estimates of export (Fig. 3B). These storms were rarely encountered during the collection of grab seston. During the first year, 23.5% (WS 53) to 41.1% (WS 55) of the sample collection intervals were influenced by storms (i.e. maximum − minimum discharge equals or exceeds 2 $L \cdot s^{-1}$ in a 24-h period). However, these intervals represented 50–66% of annual export as estimated by continuous methods (Table 5). The second year of study was influenced by a severe drought and major storms were less frequent than during year 1. However, the influence of these storms on export increased during year 2, with 71–79% of annual export occurring in collection intervals which included storms.

Export concentrations derived from continuous (barrel) and discrete (grab) methods also show the influence of storms (Table 6). The concentrations derived from barrel samplers (i.e. export ÷ total discharge) are always higher than those measured by discrete methods because barrel estimates include storms. Mean annual concentrations derived from barrels were higher for the drought year than for year 1 whereas grab estimates for year 2 were less than year 1. Maximum concentrations derived from continuous samplers were 3–7 times maximum grab concentrations. These values do not fully reflect the increase in POM concentrations which accompany a storm, since estimates from barrels are averages over the collection interval rather than over short-duration storms. POM concentrations in these streams can reach 10–100 times baseflow con-

TABLE 4. Summary of the proportion of total POM export recovered from each of the export collection barrels 1, 2, and 3 during year 1.

	WS 53			WS 54			WS 55		
	1	2	3	1	2	3	1	2	3
Mean	0.920	0.051	0.029	0.889	0.072	0.039	0.822	0.130	0.047
SE	0.009	0.006	0.003	0.010	0.007	0.004	0.011	0.008	0.005
Max.	0.978	0.172	0.073	0.966	0.198	0.127	0.933	0.246	0.164
Min.	0.759	0.011	0.010	0.727	0.022	0.012	0.643	0.049	0.005
N	34	34	34	34	34	34	33	33	33

TABLE 5. Comparison of total annual export (kg AFDM·yr^{-1}) estimates obtained using continuous (barrel) and discrete (grab) methods. Percent reduction is the percent of annual export obtained by grab estimates to that of barrel estimates [(barrel − grab estimate) ÷ (barrel estimate) × 100]. Storm export is the amount (kg) of barrel export obtained during sampling intervals which included a storm. A storm is defined to have occurred when maximum and minimum discharges differ by 2 or more L·s^{-1} in a 24-h period. Percent due to storms is the percent of annual export which is attributable to collection intervals with storms. *N* is the number of collection intervals which contained at least one storm. There are 34 collection intervals in year 1 and 26 in year 2.

	WS 53		WS 54	WS 55	
	Year 1	Year 2	Year 1	Year 1	Year 2
Annual export					
Barrel	35.40	27.83	67.63	55.86	47.07
Grab	15.80	8.08	44.22	39.35	24.78
% reduction	55.4	71.0	34.6	29.5	47.3
Storm export					
Total	15.58	19.67	36.79	35.33	37.01
% due to storms	49.8	70.7	56.1	65.7	78.6
N	8	9	11	14	11

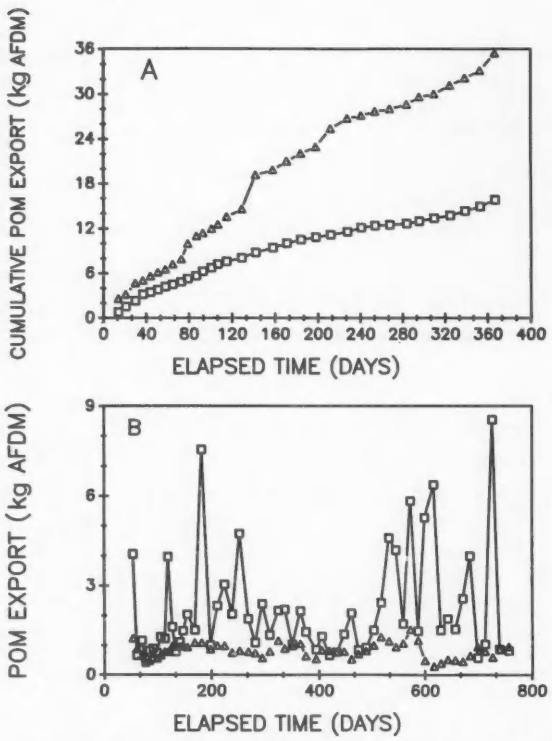

FIG. 3. Comparisons of cumulative seston export made by grab and barrel techniques for WS 53. (A) Cumulative effect of the two methods in estimating annual export during year 1 using discrete (□) and continuous (▲) methods. (B) Differences between estimates of POM export obtained from grab (□) and continuous (▲) methods for each collection interval over the 2-yr study period. Results are similar for WS 54 and WS 55.

centrations on the rising limb of the storm hydrograph (Cuffney et al. 1984), which indicates the importance of storms in producing the differences in seston concentrations between the two methods. Much more similar concentrations are produced by the two methods during periods when discharges are stable and there are no storms (see minima in Table 6).

Discussion

Influence of Storms

The present work is the first to estimate potential errors resulting from grab methods and shows that grab methods underestimate export because they underrepresent storms. Numerous investigators have noted that seston concentrations increase dramatically on the raising limb of the hydrograph and often before measurable increases in discharge occur (Fisher and Likens 1973; Bilby and Likens 1979; Gurtz et al. 1980; Fisher and Grimm 1985; Farr and Clarke 1984). This hysteresis has been attributed to the direct erosive effects of falling rain, increased subsurface flows during the falling limb of the hydrograph (Gregory and Walling 1973), and rapid suspension, during the rising hydrograph, of light materials in areas of streambed located adjacent to the stream margins at low flow (Bilby and Likens 1979). These peaks in concentration are brief and unpredictable. Consequently, even intensive sampling will underrepresent the impact of storms and underestimate export.

Significance for Other Rivers

The applicability of CHL stream data to larger rivers or to rivers in different geographical areas depends on how discharge (i.e. storm flow) and bedload characteristics relate to those of the study streams. The suitability of systematic grab sampling for estimating annual export can be related to the predictability of storms within geographic areas. Accurate results would be expected in areas, such as the arid intermountain region (e.g. Salmon River, Cummins et al. 1983), which have very predictable flows (i.e. an early summer peak corresponding to snowmelt). Results obtained in streams of the arid southwest, which have highly unpredictable flows dominated by sudden summer storms and intense floods (Busch and Fisher 1981; Fisher and Grimm 1985), would be highly inaccurate. In wetter climates (e.g. Pacific Northwest, Midwest, East, and Southeast) which have less seasonality in rainfall, there would still be a high probability of missing major storms and underestimating export. Therefore, there are only a few areas within North America where systematic grab sampling will not result in underestimates of export due to the unpredictability of storms.

The influence of storms on larger rivers is not well documented. Larger rivers have less quickflow, and peak discharge is delayed and attenuated compared with upstream reaches (Richards 1982). However, Naiman (1982) found that POM export from large rivers of boreal forest regions is significantly affected by infrequent and unpredictable storms. Richey et al. (1986) reported that concentrations of suspended sediments in the Amazon River are generally greatest on the ascending limb of the hydrograph and that peak concentrations are reached prior to peak discharge. The pattern observed for suspended sediments in the Amazon River is similar to the pattern that is typically seen in small streams (Fisher and Likens 1973; Gurtz et al. 1980; Fisher and Grimm 1985; Farr and Clarke 1984). However, in small streams the difference between peak concentra-

TABLE 6. Annual average seston concentrations (mg AFDM·L^{-1}) derived from continuous (barrel) and discrete (grab) methods. WS 54 was experimentally manipulated during year 2 and data from that year are not included here.

	WS 53		WS 54		WS 55	
	Barrel	Grab	Barrel	Grab	Barrel	Grab
Year 1						
Mean	1.945	0.839	2.319	1.613	2.068	1.546
SE	0.263	0.036	0.395	0.012	0.324	0.131
Max.	7.546	1.230	13.000	3.220	9.089	3.335
Min.	0.519	0.405	0.663	0.553	0.500	0.459
N	31	31	31	31	31	31
Year 2						
Mean	2.358	0.773			3.673	1.262
SE	0.519	0.060			1.029	0.138
Max.	6.365	1.523			21.382	3.410
Min.	0.571	0.283			0.313	0.311
N	25	25			25	25

tion and peak discharge is a matter of hours or minutes compared with months on the Amazon River.

Problems associated with measurements of bedload and the distribution of POM in the water column may rival those associated with the distribution and predictability of storms in estimating POM export. The proportion of transport moving as bedload is thought to decrease as stream size increases (Richards 1982) so that bedload is a more important problem in small high-gradient streams than in larger low-gradient rivers. Gibbs (1967) has estimated that bedload accounts for <10% of sediment transport in the Amazon River because of the overriding influence of the water column. Nonuniform distribution of POM is a more important problem in larger rivers. Curtis et al. (1979) have shown that sediment concentrations in the Amazon River are not uniformly distributed and typically increase with depth so that specialized sampling techniques are required even for grab estimates of export (Hedge et al. 1986; Richey et al. 1986). Most estimates of export in large rivers are made using grab samples collected in the water column, and bedload is often missed entirely. Our export estimates, both continuous and grab, for CHL streams were made at a flume and therefore include bedload and are not affected by nonuniform physical distributions of POM, although grab samples are affected by nonuniform temporal distributions of POM.

Whole-stream sampling methods, which were difficult and expensive in our small CHL streams, are even more impractical in larger rivers. Therefore, the affects of using grab samples to estimate annual POM export in large rivers cannot be measured directly. However, preliminary work in a fifth-order Coastal Plain stream of the southeastern United States indicates that floodplains add 39.6×10^6 kg AFDM of POM to the river each year (Cuffney 1988). Estimates of annual export using grab methods indicate an annual POM export of only 3.2×10^6 kg AFDM from this river. A substantial portion of the missing 34.6×10^6 kg AFDM may be moving undetected through the system due to the use of grab sampling techniques. This difference represents a hugh potential error in export measurement and indicates that large rivers are even more vulnerable to underestimates associated with grab techniques than are small streams.

Relationship to Stream Ecosystem Theory

Construction and analysis of organic matter budgets has been an important component in the construction of stream ecosystem theory. Problems associated with estimating POM export have important implications for organic matter budgets and the body of stream ecosystem theory which depends on accurate budgets. Organic matter budgets based on the mass balance approach will be in error if POM is underestimated, as will most of the ecological parameters derived from budgets (e.g. benthic storage, characterizations of microbial respiration, POM processing rates, and temporal, geographic, and longitudinal patterns). For example, our grab samples underestimated annual export from the three study streams by 29–71% (i.e. [barrel estimate − grab estimate] ÷ barrel estimate; Table 5). Spiralling lengths (Newbold et al. 1981) calculated using seston barrel estimates are 2–3 times longer than those calculated using grab sample estimates. Errors of this magnitude (i.e. >100%) must be considered significant and should be addressed when stream ecosystem theories are developed. However, because of the difficulty and expense, it is unreasonable to routinely advocate continuous sampling. Data obtained by grab sampling should be carefully evaluated and sampling schemes constructed to minimize the errors produced by these techniques. Careful attention must be given to infrequent and unpredictable events which occur over very small percentages of time but which have major impacts upon total export (i.e. storms).

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Impact of Heavy Metals on Insect Communities in Streams: A Comparison of Observational and Experimental Results

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This research compares effects of heavy metals on macroinvertebrate communities in outdoor experimental streams with those observed at impacted field sites. Natural assemblages of aquatic macroinvertebrates were established on substrate-filled trays which were then transferred to outdoor stream mesocosms. Exposure of these communities to low levels of copper and zinc (target concentration = 12 μg/L) significantly reduced the number of taxa, number of individuals, and abundance of most dominant taxa within 4 d. After 10 d, control streams were dominated by Ephemeroptera and Tanytarsini chironomids, whereas treated streams were dominated by Hydropsychidae and Orthocladiini. Responses of benthic communities to metals observed at the Clinch River (Russell Co., Virginia), a system impacted by copper and zinc, were similar to those in experimental streams. Ephemeroptera and Tanytarsini, which comprised 38–46% of the macroinvertebrate community at upstream reference stations, were significantly reduced at all effluent sites. As in treated experimental streams, impacted stations were dominated by Hydropsychidae and Orthocladiini. The similarity of our experimental results to those obtained from Clinch River field sites suggests that outdoor stream mesocosms may be employed to predict macroinvertebrate community responses to heavy metals.

La présente recherche compare les effets des métaux lourds sur les communautés de macro-invertébrés vivant dans des cours d'eau expérimentaux extérieurs, comparativement à ceux observés dans les emplacements *in situ* touchés. On a formé des groupements naturels de macro-invertébrés aquatiques sur des plateaux remplis de substrat qui ont été ensuite placés dans des mésocosmes de cours d'eau extérieurs. L'exposition de ces communautés à de faibles concentrations de cuivre et de zinc (concentration cible = 12 μg/L) a diminué de façon significative le nombre de taxons, le nombre d'individus et l'abondance des taxons les plus dominants en 4 d. Après 10 d, les cours d'eau témoins ont été surtout peuplés par des chironomidés de la famille des éphéméroptères et des tanytarsini, tandis que les cours d'eau touchés ont été surtout peuplés par des hydropsychidés et des orthocladiini. Les réactions des communautés benthiques aux métaux qui ont été observées dans la rivière Clinch (Russell Co., Virginie), un système touché par le cuivre et le zinc, étaient semblables à celles observées dans les cours d'eau expérimentaux. Il y a eu une diminution significative des populations d'éphéméroptères et de tanytarsini, constituant 38–46 % de la communauté des macro-invertébrés des stations témoins en amont, dans tous les emplacements soumis à l'effet des métaux. Comme dans le cas des cours d'eau expérimentaux traités, les stations touchées par les métaux ont été surtout peuplées par des hydropsychidés et des orthocladiini. D'après la similitude de nos résultats expérimentaux comparativement à ceux obtenus à certains endroits de la rivière Clinch, il serait possible d'utiliser des mésocosmes de cours d'eau d'eau extérieurs pour prévoir la réaction des communautés de macro-invertébrés aux métaux lourds.

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Production of heavy metals and their discharge into aquatic receiving systems have increased greatly in recent years (Moore and Ramamoorthy 1984). The effects of these effluents on aquatic invertebrates have been well documented in the laboratory (Warnick and Bell 1969; Brown 1977; Spehar et al. 1978; Kosalwat and Knight 1987). Although results of these experiments show considerable variation among species, in general most aquatic invertebrates are quite sensitive to heavy metals (Hodson et al. 1979). Several investigators, however, have noted the limitations of laboratory bioassays and have suggested that these tests be supplemented with more environmentally realistic procedures, including field sampling and experimentation (Cairns 1983, 1986; Odum 1984; Kimball and Levin 1985). Traditionally, most field research on the impact of heavy metals has been purely descriptive (Sprague et al. 1965; Armitage 1980; Ramusino et al. 1981; LaPoint et al. 1984; Chadwick et al. 1986; Clements et al. 1988b), and consequently, few attempts have been made to predict changes in macroinvertebrate communities exposed to these effluents. An important exception to the descriptive approach employed by most field researchers is the work conducted at Shayler Run by Winner et al. (1975, 1980). These investigators monitored changes in macroinvertebrate communities exposed to copper (Cu) in experimentally polluted streams and concluded that these communities showed predictable changes in structure along a gradient of heavy metals stress.

While such experimental manipulations are the most direct method of determining cause and effect relationships between toxicants and macroinvertebrate community structure (LaPoint et al. 1984), logistical and economic considerations make this

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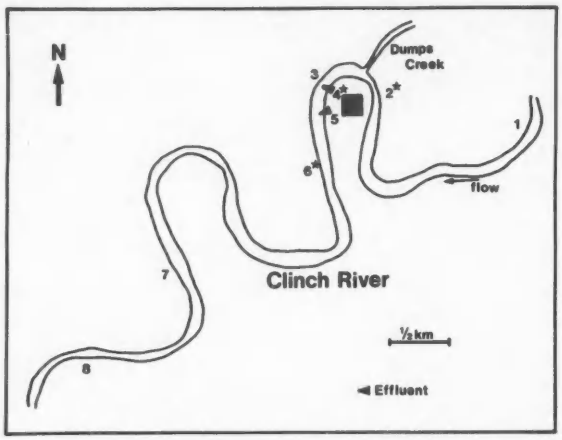

FIG. 1. Sampling stations at the Clinch River. Stations marked with a star were compared with experimental streams. Arrowheads refer to location of effluent discharges.

an unlikely approach on a large scale. This conclusion is particularly relevant given the recent emphasis on development of site-specific water quality criteria (Carlson et al. 1986; Van Hassel and Gaulke 1986). An alternative approach, advocated by Odum (1984), involves the use of mesocosms or "bounded and partially enclosed outdoor experimental" systems.

In previous experiments (Clements et al. 1988a), we exposed natural assemblages of aquatic insects to Cu in laboratory streams and showed that community-level parameters (number of taxa, number of individuals) were highly sensitive to this toxicant. We also suggested that this approach may be employed to predict effects of heavy metals in the field. Here we employed a similar approach and investigated macroinvertebrate community responses to heavy metals in the field and in outdoor experimental streams. Our specific objectives were to (1) document structural alterations in macroinvertebrate communities at field sites impacted by Cu and zinc (Zn) and (2) compare the impact of these effluents on macroinvertebrate communities in the field with those in experimental streams dosed with Cu and Zn.

Materials and Methods

Clinch River Biomonitoring

To document the impact of heavy metals on aquatic insect communities in the field, eight sampling stations were selected at the Clinch River, a fourth-order tributary to the Tennessee River located in Russell County, Virginia (Fig. 1). The river is ~60 m wide and depth ranges from 0.5 to 0.8 m at sampling stations. Substrate is dominated by large pebble and intermediate cobble. Reference stations 1 and 2 were located upstream, and reference station 3 was located directly across from a coal-fired electric generating plant. Station 4 was located 50 m downstream of a cooling tower blowdown effluent, and station 5 was located 30 m below a second, low-volume waste discharge. These two stations represented high-effluent sites, whereas station 6, located 1.0 km farther downstream, was noted as a low-effluent site. Recovery stations 7 and 8 were located 3.0 and 4.5 km downstream of the plant, respectively.

In August 1986, six substrate-filled trays (10 × 10 × 6 cm) containing pebble and small cobble were placed at each of these stations. After 30 d of colonization, all trays were collected by placing a 500-μm-mesh net directly downstream and then removing the tray from the stream. Previous studies at the Clinch River (Clements et al. 1988b) showed that only six of these trays were necessary to detect a 15% reduction in number of individuals and a 12% reduction in number of taxa at effluent stations. Contents of each tray were washed through a 500-μm sieve and preserved in 10% formalin. In the laboratory, organisms were sorted in white enamel pans and identified to the level of genus, species, or, for Chironomids, tribe.

TABLE 1. Water chemistry data from the Clinch River and from outdoor experimental streams. Field values represent the means of weekly samples (n = 5) collected in August and September 1986. Experimental stream data (n = 8) were collected on days 36 and 42. Stations 2, 6, and 4 refer to reference, low-, and high-effluent sites, respectively. Standard deviations are given in parentheses. nd = not detected; — = no data collected.

	Clinch River								Experimental streams		
	1	2	3	4	5	6	7	8	Control	Low	High
Temperature (°C)	22.4 (1.5)	22.6 (1.9)	21.6 (1.7)	21.8 (1.8)	22.3 (1.4)	22.7 (1.6)	22.6 (1.3)	21.0	22.1 (1.5)	22.4 (1.8)	22.0 (1.4)
Dissolved oxygen (mg/L)	8.1 (0.7)	8.0 (0.8)	7.9 (0.7)	7.9 (0.6)	7.9 (0.9)	7.9 (0.8)	8.1 (0.8)	8.2	9.3 (0.9)	8.9 (1.0)	8.4 (0.8)
Current (cm/s)	12.9 (3.6)	45.9 (7.2)	35.5 (5.8)	47.5 (7.1)	30.2 (3.3)	46.0 (6.3)	33.8 (7.8)	38.2	42.0	42.0	42.0
pH	8.40 (0.19)	8.45 (0.12)	8.43 (0.21)	8.36 (0.16)	8.17 (0.15)	8.41 (0.20)	8.32 (0.16)	8.46	8.91 (0.21)	8.93 (0.22)	8.90 (0.21)
Conductivity (μS/cm)	298 (21)	299 (20)	319 (21)	364 (24)	357 (229)	327 (18)	323 (16)	312	145 (11)	146 (13)	146 (15)
Hardness (mg/L)	159 (16)	156 (122)	170 (17)	186 (12)	185 (18)	164 (21)	166 (21)	168	90 (12)	85 (9)	85 (11)
Alkalinity (mg/L)	145 (26)	156 (16)	156 (19)	117 (24)	143 (29)	162 (16)	160 (15)	141	56 (8)	59 (11)	57 (11)
[Cu] (μg/L)	nd	3 (6)	nd	105 (22)	47 (16)	9 (7)	nd	—	nd	12 (4)	20 (5)
[Zn] (μg/L)	14 (21)	10 (10)	12 (8)	81 (17)	42 (12)	18 (13)	6 (7)	—	nd	15 (3)	27 (7)

[a] n = 1.

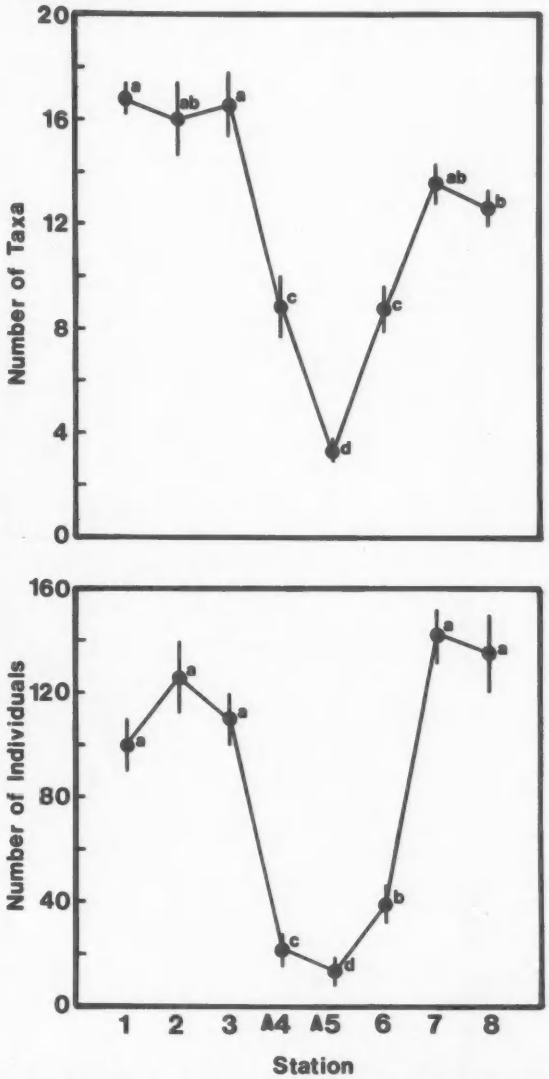

FIG. 2. Number of taxa and number of individuals at sampling stations in the Clinch River. Each point represents the mean number per tray ($n = 6$) ±SE. Means with the same letter were not significantly different. Arrowheads refer to location of effluent discharges.

Experimental Streams and Clinch River Comparison

Benthic communities for the experimental streams studies were established on trays placed at reference station 2 in the Clinch River. To determine the amount of time necessary to obtain equilibrium communities on these substrates, six trays were sampled from station 2 after 6, 12, 18, 30, 36, and 42 d of colonization. All samples were collected and processed as described above. On day 30, 48 colonized trays were removed and placed into 12 separate 7-L coolers (four trays per cooler) filled with stream water. Each cooler was supplied with an airstone and attached to a 12-V air pump. Trays were transferred to the Glen Lyn Research Site, located on the banks of the New River in Giles County, Virginia, and the trays in each cooler were placed into a separate experimental stream. Each oval, flow-through stream (76 × 46 × 14 cm) was supplied with unaltered water drawn from the New River at a rate of 1.6 L/min, resulting in a turnover time of 13 min. Current in the streams was provided by paddle wheels, which maintained a constant velocity of 42 cm/s.

After 2 d of acclimation, streams were randomly assigned to one of three treatments: controls (ambient Cu and Zn levels), low-metal (12 μg Cu and Zn/L) and high-metal (50 μg Cu and Zn/L). Target values of Cu and Zn in high-metal streams were ~50% lower than concentrations previously measured at station 4, the high-effluent site. Reduced target concentrations were used in experimental streams because of lower water hardness of the New River, which generally increases toxicity of metals (Winner and Gauss 1986). Stock solutions of copper and zinc sulfate were dripped into each treated stream at a rate of 6 mL/min. On days 36 and 42 (after 4 and 10 d of exposure to metals), two trays from each stream were removed and processed as described above. Trays collected from control streams were compared with trays from reference station 2 at the Clinch River on day 36 and 42. Similarly, trays from low- and high-metal streams were compared with those collected from low- (station 6) and high- (station 4) effluent sites on these same days.

Water Quality

Water temperature, dissolved oxygen, current velocity, pH, conductivity, hardness, alkalinity, and metal concentrations were measured weekly at all field sites, except for station 8. Water samples were collected from this station only on day 30, and metal concentrations were not determined. Water quality data were collected from each experimental stream on days 36 and 42. Concentrations of total Cu and Zn were measured with a flameless atomic absorption spectrophotometer (detection level = 3 μg/L).

Statistical Analyses

Design of the experimental stream studies included three treatments, four replicate streams, and two subsamples within each stream. Differences between treatments in these streams and between sampling stations in the field were determined using one-way ANOVA. All analyses were performed on $\ln(n+1)$ transformed data to stabilize the variances. If differences in the overall F-test were detected ($p < 0.05$), Duncan's multiple range test was used to determine which treatments (or stations) were significantly different from others.

We estimated equilibrium numbers of individuals and taxa for the colonization study using a nonlinear regression procedure. Colonization data were fitted to a negative exponential growth equation

$$N = N_{eq}(1 - e^{-mt})$$

where N = number of individuals, N_{eq} = equilibrium number of individuals, m = colonization rate, and t = time.

Results

Water Quality

Water temperature, dissolved oxygen, current velocity, and pH were similar at the Clinch River and in experimental streams (Table 1). Conductivity, alkalinity, and hardness were, however, considerably greater in the Clinch River.

Mean Cu and Zn concentrations at effluent stations in the Clinch River were generally higher than in treated experimental

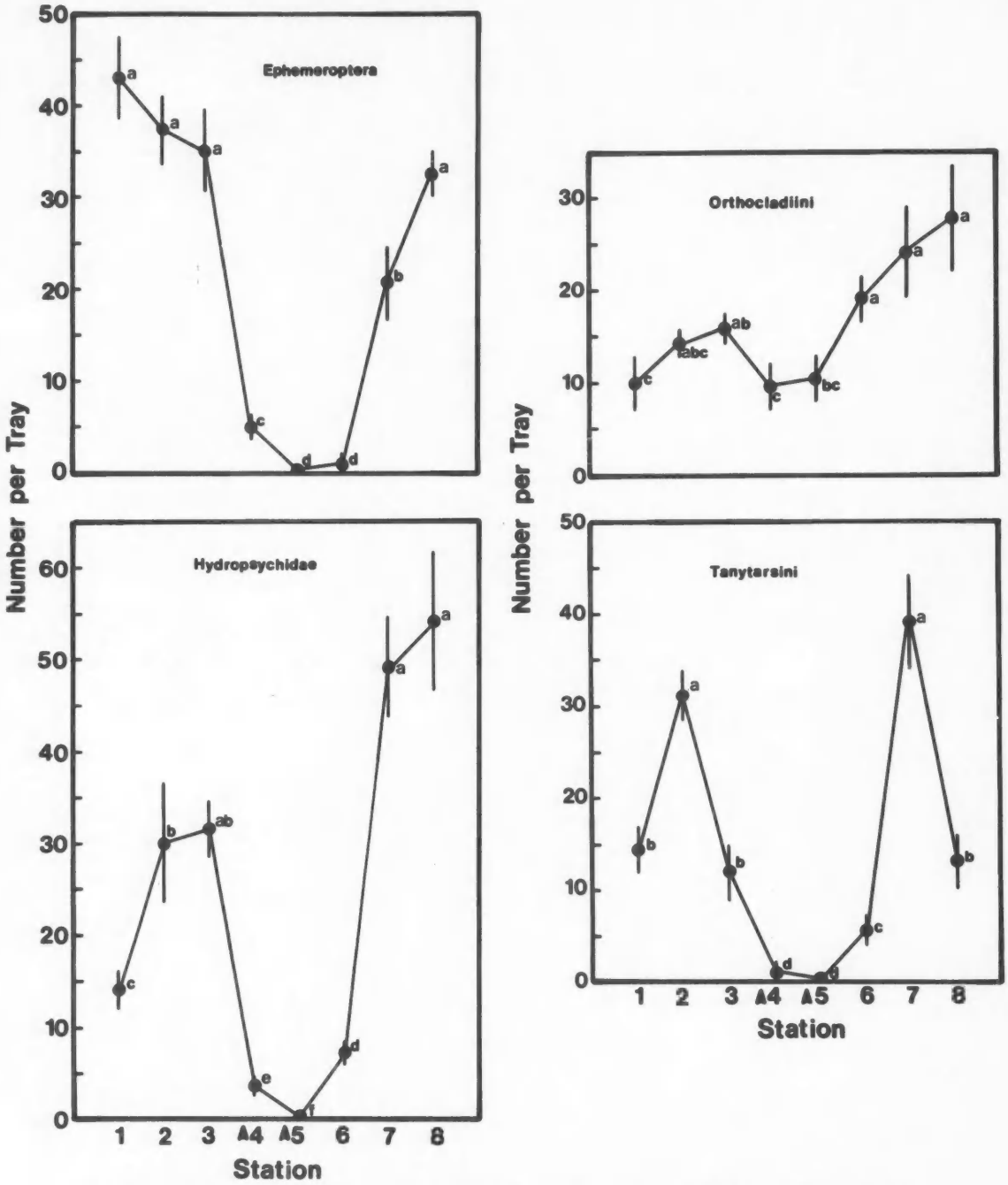

FIG. 3. Abundance of dominant groups of organisms at sampling stations in the Clinch River. Key same as Fig. 2.

streams. Highest concentrations in the field were recorded from stations 4 and 5. Metal concentrations were greatly reduced at station 6, the low-effluent site, and were comparable with upstream reference sites at station 7. Measured concentrations of Cu and Zn in low-metal experimental streams approximated target values, whereas measured values were ~50% less than target concentrations in high-metal streams.

Clinch River Biomonitoring

There were significantly fewer taxa and individuals per tray at effluent stations in the Clinch River than at upstream refer-

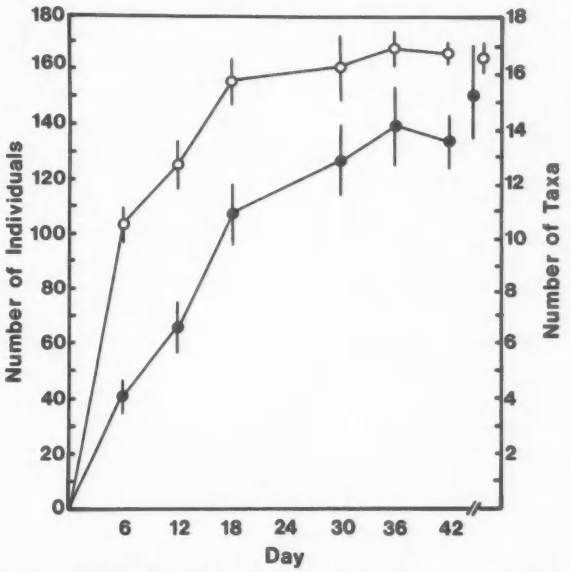

FIG. 4. Colonization of introduced substrates at reference station 2. Points represent the mean number of individuals (solid circles) and taxa (open circles) per tray ($n = 6$) ± SE. Estimated equilibrium number of individuals and taxa, represented by points beyond day 42, are also included.

ence sites (Fig. 2). The number of taxa increased at recovery stations 7 and 8, but was lower than at reference stations. Macroinvertebrate abundance also increased downstream and was slightly, although not significantly, greater at recovery stations than at reference sites. This increase was primarily the result of greater abundance of Hydropsychidae and Orthocladiini at stations 7 and 8.

Except for Orthocladiini, the basic pattern of Fig. 2 was seen for all dominant groups (Fig. 3). The greatest effects were observed on Ephemeroptera, which, in contrast with other groups, did not recover at station 7. Tanytarsini chironomids were also highly sensitive to these effluents; however, their distribution among both reference and recovery stations was highly variable. Orthocladiini chironomids were more tolerant of heavy metal effluents than other groups. The only pairwise comparison of stations showing significant differences among reference and high-effluent sites was between stations 3 and 4. Abundance of Orthocladiini and Hydropsychidae was significantly greater at recovery stations than at upstream reference sites.

Comparison of Clinch River and Experimental Streams

Colonization of trays used for the experimental streams studies was rapid during the first 18 d, and then gradually levelled off (Fig. 4). Both the observed number of taxa and individuals per tray were within the 95% confidence intervals of estimated equilibrium values by day 30.

Exposure of equilibrium communities to Cu and Zn in experimental streams significantly reduced macroinvertebrate abundance and number of taxa within 4 d (Fig. 5). After 10 d, community responses to metals in experimental streams were similar to those at the Clinch River. Although abundance was greater in experimental streams than at corresponding field stations, the shapes of the curves for the experimental streams and Clinch River field sites were identical by day 42.

The responses of dominant groups of aquatic insects (Ephemeroptera, Hydropsychidae, Orthocladiini, and Tanytarsini) to heavy metals in experimental streams were also similar to those observed at the Clinch River, particularly on day 42 (Fig. 6). Ephemeroptera and Tanytarsini were the most sensitive organisms examined. Both groups were significantly reduced in low-metal streams and at the low-effluent site on days 36 and 42. Hydropsychidae were more tolerant of heavy metals than either Ephemeroptera or Tanytarsini, particularly in experimental streams. On day 36, caddisflies were reduced by only 35% in low-metal streams compared with 81% for these more sensitive groups.

The response of Orthocladiini chironomids to heavy metals at the Clinch River and in experimental streams was quite different from that observed for other groups. In the field, abundance was similar at reference and low-effluent sites on both days. In treated experimental streams, abundance increased between days 36 and 42 but decreased in controls. As a result, the number of Orthocladiini was significantly greater in low-metal streams than controls on day 42.

The percent composition of these dominant groups in control and treated streams was similar to that at reference and effluent sites, respectively (Fig. 7). Sensitive taxa, such as Tanytarsini, *Isonychia bicolor*, *Stenonema modestum*, and *Baetis brunneicolor*, comprised 29–39% of the total organisms in control streams and at the reference station in the field. In contrast, at the low-effluent site and in low-metal streams, these groups comprised only 3–17% of total abundance. In treated streams and at effluent sites in the field, these sensitive taxa were replaced by more tolerant groups, such as Orthocladiini and Hydropsychidae, which accounted for 60–90% of total individuals. Owing to the reduced total number of organisms at the high-effluent site, percent composition of *B. brunneicolor* and *I. bicolor* was artificially elevated. Although the actual numbers of these organisms were greatly reduced at this station (only two to three per tray) compared with the reference site, the percent composition was similar.

Discussion

Results of our experimental studies and field biomonitoring support the findings of other researchers who have shown major alterations of macroinvertebrate community structure in streams receiving heavy metals (Winner et al. 1980; LaPoint et al. 1984; Chadwick et al. 1986; Clements et al. 1988b). More importantly, the similarity of our experimental results to those obtained from the Clinch River indicates that macroinvertebrate responses to heavy metals are, as suggested by Winner et al. (1980), highly predictable. Within 10 d, number of organisms, number of taxa, and abundance of dominant groups in control and treated experimental streams reflected values observed at reference and effluent stations in the Clinch River, respectively. Responses to Cu and Zn in experimental streams also occurred rapidly, as macroinvertebrate abundance was reduced by 57% within 4 d in low-metal streams. These findings suggest that our approach may provide a cost-effective alternative to actual field experimentation for predicting the impact of toxicants on benthic communities.

Total macroinvertebrate abundance and abundance of most dominant taxa were greater in control experimental streams than at the reference station on both sampling days. In addition,

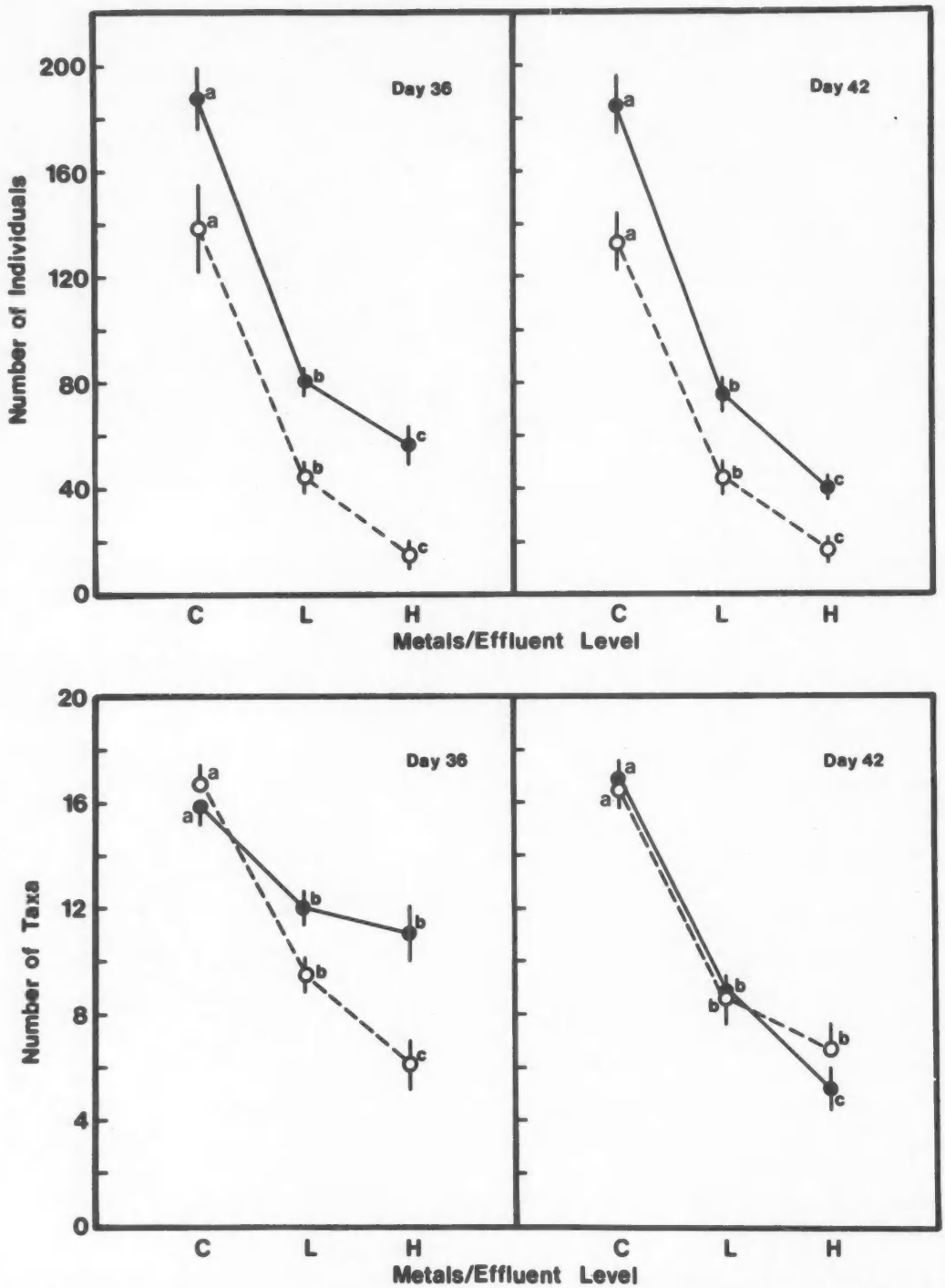

FIG. 5. Effects of heavy metals on macroinvertebrate abundance and number of taxa in experimental streams (solid lines) and at the Clinch River (broken lines) on days 36 and 42. C, L, and H refer to control, low-, and high-metal/effluent levels, respectively. Each point represents the mean ± SE. Means with the same letter were not significantly different.

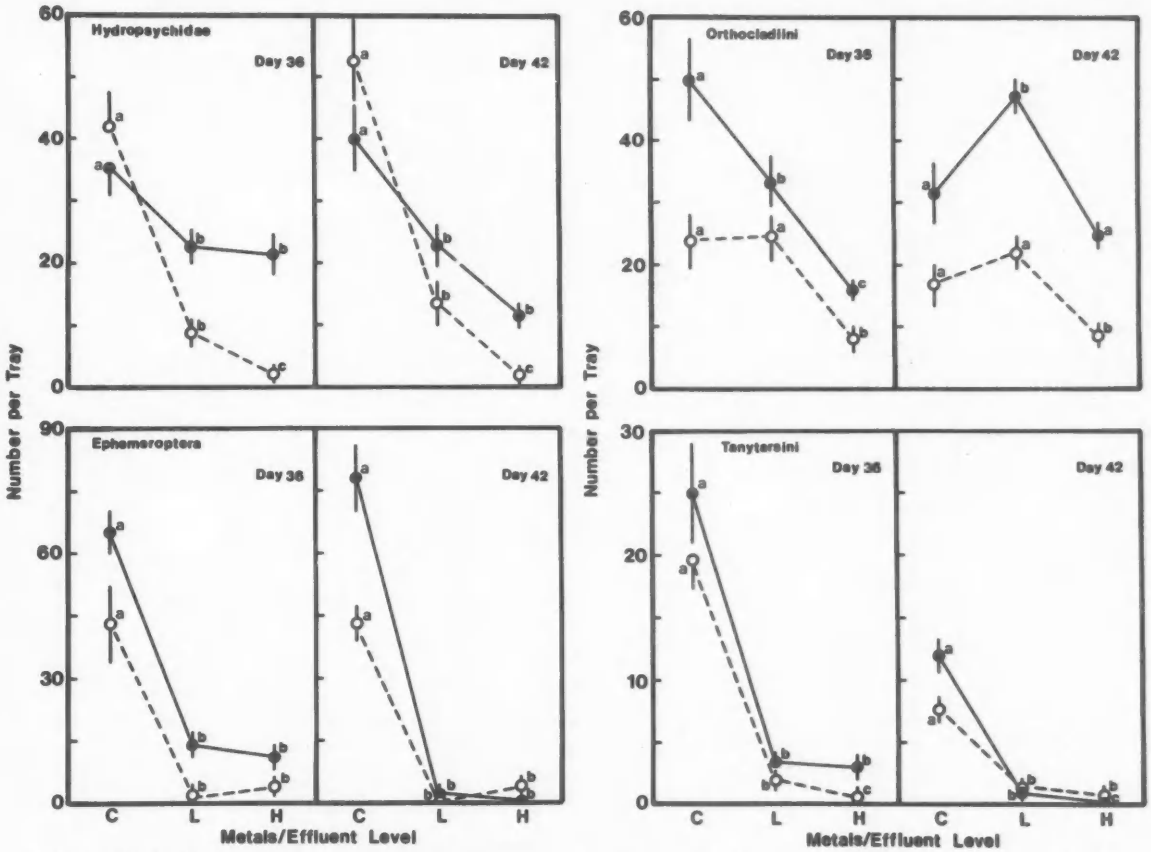

FIG. 6. Effects of heavy metals on dominant groups of organisms in experimental streams and the Clinch River. Key same as Fig. 5.

abundance of some groups increased in control streams (Hydropsychidae, Ephemeroptera) or treated streams (Orthocladiini) between days 36 and 42. Recent experiments (W. H. Clements, unpubl. data) have shown that these apparent increases were not the result of either immigration via diluent water or oviposition by adults. Thus, these organisms must have been present on the trays when placed in the streams but not sampled effectively. The most likely explanation for these observed increases was that early instars that passed through our 500-μm sieve on day 30 or 36 grew during the course of these experiments and were retained on the next sampling.

Responses of Dominant Macroinvertebrates to Heavy Metals

In general, our experimental and observational results support the findings of other researchers who have reported increased tolerance of heavy metals from mayflies to caddisflies to chironomids (Winner et al. 1980; Wiederholm 1984). In our study, mayflies were eliminated after 10 d of exposure in low-metal streams and were the only group which did not recover at station 7 in the field. In contrast with the above predictions, however, Tanytarsini chironomids were quite sensitive to heavy metals, a finding that has been reported elsewhere (Anderson et al. 1980). Caddisflies, which were considerably less sensitive of heavy metals than either Ephemeroptera or Tanytarsini, were significantly more abundant at recovery stations than reference sites in the field. Sprague et al. (1965) also reported increased abundance of caddisflies at metal-impacted sites. These findings, in addition to our experimental results that showed that caddisfly abundance did not vary in low-metal streams between days, indicate that these organisms can tolerate moderate levels of metal pollution.

Several investigators have noted the tolerance of chironomids, particularly Orthocladiini, to heavy metals (Surber 1959; Sprague et al. 1965; Winner et al. 1975, 1980; Armitage 1980; Waterhouse and Farrell 1985; Chadwick et al. 1986). Surber (1959) reported increased abundance of *Cricotopus bicinctus* at sites receiving Cu and chromium. Winner et al. (1980) also found that two species of Orthocladiini, *C. bicinctus* and *C. infuscatus*, dominated stations impacted by heavy metals. In our study, Orthocladiini were the dominant organisms at all effluent stations in the field and in treated experimental streams. Thus, it appears that the response of some Orthocladiini to heavy metals may be analogous to that of some oligocheates (e.g. *Tubifex tubifex* and *Limnodrilus hoffmeisteri*) to organic pollution.

Although tolerance of this group for heavy metals may explain their dominance relative to other, more sensitive organisms, it does not explain why abundance was greater in treated experimental streams and at effluent sites than in controls. Increased abundance of Orthocladiini may have resulted from reduced numbers of potential competitors that were eliminated from treated streams and effluent sites. Alternatively, these

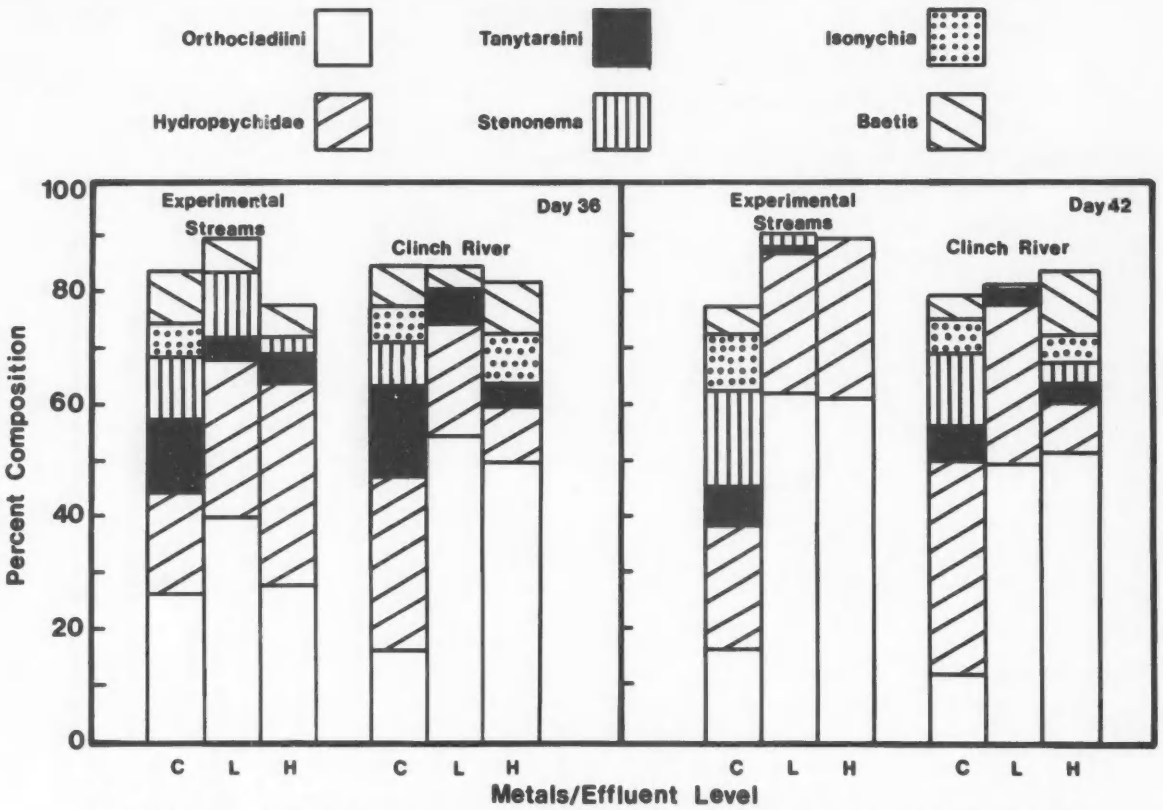

FIG. 7. Relative abundance of dominant taxa in experimental streams and at the Clinch River. C, L, and H same as Fig. 5.

organisms may have responded to increased abundance of a particular resource. Surber (1959) noted that Orthocladiini feed on resistant blue-green algae that often dominate metal-polluted areas. At effluent sites in the Clinch River and in treated experimental streams, blue-green algae were abundant and may have provided a resource not available at reference sites and in control streams. The unique response of Orthocladiini to metal effluents and their potential usefulness as an indicator of metal pollution require further investigation.

Advantages of This Approach

Presently, most multispecies toxicity research involves simply testing groups of aquatic organisms simultaneously, with little concern for species interactions (Mount 1985). These assemblages are often highly synthetic and are frequently selected out of convenience and need for standardization rather than ecological relevance. Niederlehner et al. (1985) discussed the importance of using naturally derived communities of organisms for toxicity testing. We feel that the main advantage of our procedure is the ability to predict responses of macroinvertebrate communities to toxicants. For example, this approach could be employed to validate site-specific water quality criteria prior to the actual release of an effluent. This method could also be useful in situations where logistical problems complicate direct measurement of impact using field sampling.

Our approach is also more environmentally realistic than that employed in previous studies, as organisms were collected with their natural substrate and placed into outdoor experimental streams receiving unaltered river water. Since these trays accumulated both detritus and periphyton during colonization (W. H. Clements, pers. obs.), a natural food source was available. Finally, our approach will provide an opportunity to test organisms that are rarely included in standard laboratory bioassays. Many of the taxa that colonize these trays, especially early instars of some mayflies, cannot be tested using conventional procedures because of difficulties collecting and maintaining them in the laboratory. These early life stages of aquatic insects often comprise a significant portion of the benthic community and are usually quite sensitive to pollution (Hodson et al. 1979). It therefore follows that these organisms should be included in toxicity testing and establishment of water quality criteria.

Acknowledgments

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Sediment Control of Soluble Reactive Phosphorus in Hoxie Gorge Creek, New York

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Klotz, R. L. 1988. Sediment control of soluble reactive phosphorus in Hoxie Gorge Creek, New York, Can. J. Fish. Aquat. Sci. 45: 2026–2034.

Stream sediments were found to regulate the soluble reactive phosphorus (SRP) of stream water by geochemical processes. This conclusion was based on sediment analysis, laboratory sorption experiments, and measurement of the equilibrium phosphorus concentration (EPC). EPC is the concentration of P in the water at which there is neither sorption nor desorption of P by the sediments. At low flow conditions, streamwater SRP was highly correlated with EPC at six sites along Hoxie Gorge Creek ($r = 0.979$). EPC was inversely related to the ionic strength of the equilibrating solution, with Ca^{2+} producing larger changes than Na^{+}. Minimum EPC values occurred near the neutral pH of the stream water and increased sharply in acidic and basic solutions. Also, EPC was negatively correlated with the exchangeable Al content of the sediments at the six sites. These data are consistent with a mechanism previously verified for soils in which solution cations displace exchangeable Al(III) from sediments; hydrolyzed Al(III) reacts with phosphate and removes it from solution. EPC and streamwater SRP were lower at sites with sediments that had higher concentrations of P-binding sites, despite also having higher sediment P.

L'auteur a trouvé que les sédiments de cours d'eau régulaient, par processus géochimiques, le phosphore réactif soluble (PRS) présent dans l'eau. Cette conclusion repose sur une analyse des sédiments, des expériences de sorption réalisées en laboratoire et la mesure de la concentration de phosphore en équilibre (CPE). La CPE est la concentration de P dans l'eau à laquelle il n'y a ni sorption ni désorption de P par les sédiments. En condition de faibles débits, le PRS de l'eau présentait une corrélation élevée avec le CPE en six points du ruisseau Hoxie Gorge ($r = 0{,}979$). La CPE présentait une relation inverse avec le pouvoir ionique de la solution d'équilibre, le Ca^{+2} produisant des modifications plus importantes que le Na^{+}. Les valeurs CPE minimales étaient notées au voisinage du pH neutre du cours d'eau et augmentaient nettement en solutions acides ou basiques. De plus, la CPE présentait une corrélation négative avec la teneur en Al échangeable des sédiments, cela aux six points. Ces données sont cohérentes avec un mécanisme déjà noté dans les sols où les cations en solution déplacent l'Al(III) échangeable des sédiments; l'Al(III) hydrolysé réagit avec le phosphate et l'élimine de la solution. La CPE et la teneur en PRS de l'eau du cours d'eau étaient inférieures aux points où les sédiments présentaient de plus fortes concentrations de sites liant le P même si la teneur en P des sédiments était plus élevée.

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Sediments play an important role in the P dynamics of streams. The concentration of dissolved P in the water that is due to sediment sorption and desorption processes has been called the equilibrium phosphorus concentration (EPC) and is determined by laboratory equilibration of the sediments in a defined medium. Previous workers found that sediments rapidly sorbed added P and concluded that the close agreement between EPC and streamwater dissolved P indicated that sediments may regulate the dissolved P concentration (Taylor and Kunishi 1971; Meyer 1979). However, positive correlations between EPC and dissolved streamwater P do not by themselves constitute sufficient evidence to prove a cause and effect phenomenon.

Development of a model explaining EPC in streams is necessary before researchers can positively conclude that sediments regulate streamwater P; no model presently exists. Initial steps in determining a mechanism for EPC have been made by correlating EPC with various sediment fractions, but little definitive information has resulted. Meyer (1979) separated sediments from Bear Brook into coarse-grained sandy sediments of low (1%) organic content and fine-grained silty sediments of higher (8%) organic content, but did not find a significant difference in EPC. Hill (1982) compared sediments from two streams with different organic content and size fractions, but found no difference in EPC. McAllister and Logan (1978) also found no correlations between EPC and a number of sediment characteristics of the Maumee River of Ohio, including Fe, Al, "available" P, fine and total clay, and organic content. However, the suspended sediments in the Maumee River did exhibit a positive correlation between EPC and calcite content (Green et al. 1978).

This paper proposes a mechanism for EPC in a stream. Correlations between EPC in Hoxie Gorge Creek and certain sediment characteristics as well as laboratory sorption and desorp-

tion experiments provided the necessary evidence for the model. The results show that a standard method for measuring EPC is invalid.

Study Area

Longitudinal studies were done at six sites along Hoxie Gorge Creek, New York (Fig. 1). Sites 4a and 4b were surrounded by 2–8% slopes with poorly drained, strongly acid soils derived from glacial till with fragipan at depths between 20 and 35 cm. Site 4c was surrounded by alluvial land made up of soils that were so intermingled that it was not feasible to map them separately. Sites 4d–4f were located in the gorge area with walls of 25–55% slope, well-drained soils formed in thin glacial till, and a depth to bedrock generally between 0.8 and 1.0 m (USDA 1961).

Methods

Streamwater samples were collected in acid-cleaned, 1-L polyethylene bottles and stored on ice until returned to the laboratory. Soluble reactive phosphorus (SRP) was determined in duplicate on filtered (0.45-μm Millipore type HA, acid cleaned) streamwater samples the day of collection by the ascorbic acid method (APHA 1975). When Ca was measured, alloquots of the same filtered samples were analyzed with a Perkin-Elmer model 303 atomic absorption spectrophotometer. A composite sediment sample totalling 1 L was collected from the upper 7 cm of sediments at 10 locations at each site and either used fresh the day of collection for EPC and other P sorption experiments or dried (80°C) and stored for subsequent determination of sediment characteristics.

EPC was determined basically by the technique of White and Beckett (1964), as modified by Taylor and Kunishi (1971) and described by Meyer (1979). Typically, duplicate sieved (2-mm mesh) sediment subsamples were incubated 1 h at 20°C in 50 mL of 400 mg $Ca \cdot L^{-1}$ ($CaCl_2$) solution spiked with $KH_2PO_4^{3-}$. The $CaCl_2$ concentration was varied in later experiments, and in one, $CaCl_2$ was replaced by NaCl. Initial P concentrations were 0, 5, and 10 $\mu g \cdot L^{-1}$ for sediments with low EPC values and 0, 10, and 25 $\mu g \cdot L^{-1}$ for conditions producing higher measured EPC values. Flasks were shaken vigorously for 5 s every 10 min during the incubation. The aqueous and sediment phases were separated by filtration through acid-cleaned 0.45-μm membrane filters (Millipore type HA) and SRP determined on the filtrate by the ascorbic acid method (APHA 1975). For the 24 October 1985 samples, 6 mL of sieved sediments was used, but subsequent experiments showed that sediment volume did not influence EPC; therefore, smaller sediment volumes were used as noted to aid in filtration. Measured sediment subsamples were dried at 80°C to express sorption per unit dry weight. To determine if P precipitated from solution with Ca at the high Ca concentration used in the solutions for some EPC analyses, 25 $\mu g \, P \cdot L^{-1}$ solutions were spiked with 0, 15, 30, and 400 mg $Ca \cdot L^{-1}$ ($CaCl_2$) at pH 7.25 (the pH at site 4f). Duplicate flasks were treated exactly as were flasks for EPC measurements, except no sediments were present.

The ability of the sediments to sorb large amounts of P was determined as the phosphate sorption index, a measure of the phosphate buffering capacity of sediments (Bache and Williams 1971). The index was calculated as $X/\log_{10}C$, where X is P

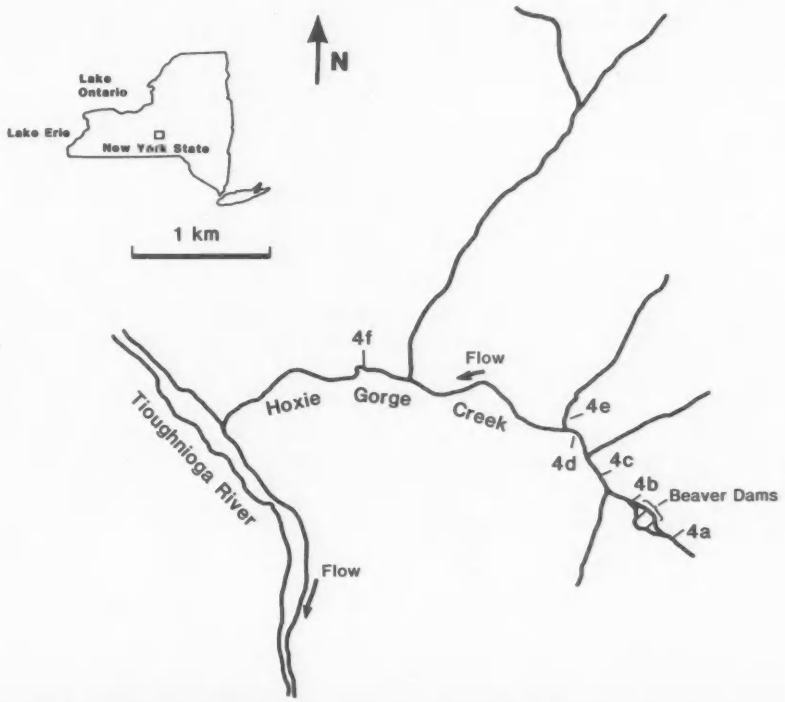

FIG. 1. Map of the six sites along Hoxie Gorge Creek located in Cortland County, New York, USA.

sorbed (in micrograms per gram dry weight sediment) from a concentration of 2000 μg $P \cdot L^{-1}$ and C is the final P concentration (in micrograms per litre) in the solution after 1 h (for details see Klotz 1985). A high value for the index indicates that a large amount of P can be sorbed by the sediment without increasing the P concentration in the water at equilibrium. The ability of site 4a and 4f sediments to sorb a range of P concentrations was determined by incubating 3 mL of sediments in 50 mL of $CaCl_2$ solution (20 mg $Ca \cdot L^{-1}$) spiked with $KH_2PO_4^{3-}$ in duplicate. Initial phosphate concentrations were 0.031, 0.31, 1.55, 3.1, 7.75, and 15.5 mg $\cdot L^{-1}$ for site 4a sediments and 0.031, 0.155, 0.31, 0.62, 0.93, 1.55, and 3.1 mg $\cdot L^{-1}$ for site 4f sediments.

The effect of pH and EPC and the phosphate sorption index was measured in solutions buffered with acetic acid – sodium acetate in the acidic range and with Trizma HCl and Trizma Base in the basic range.

The relative importance of biological versus geochemical processes on EPC was studied by comparing the EPC values of autoclaved and living sediments from both sites 4b and 4f. Sediments collected 28 January 1987 were sieved and autoclaved 15 min at 121°C and 1.02 atm (103.352 kPa). Both autoclaved and living sediments were rinsed twice using centrifugation in 20 mg $Ca \cdot L^{-1}$ solution, and EPC determinations were performed by standard methods using 3 mL of sediments in 50 mL of solution.

A number of characteristics considered potentially important for P sorption were determined for sediments collected on 24 October 1985. Exchangeable Fe and Al, defined as being removable by neutral salt solution (Bohn et al. 1979), were obtained by incubating 0.2 g of sediments in 50 mL of 1 N neutral KCl solution (Hall and Baker 1971) on a shaker for 45 min, followed by filtration through acid-cleaned 0.45-μm membrane filters (Millipore type HA). Acid-extractable Fe and Al were obtained by the technique used by Meyer (1979). Following the pretreatments, exchangeable and acid-extractable Al and Fe concentrations were determined on the filtrates by the ferronorthophenanthroline method (Rainwater and Thatcher 1960). Sediment Ca was extracted by incubating 0.5 g of sediments in 10 mL of concentrated HCl for 1 h; the filtrate was analyzed by atomic absorption spectrophotometry. Carbonate analyses were done on finely ground sediments using a gas chromatograph by the syringe gas-stripping method of Stainton (1973). Major element compositions were determined for 345 sediment particles from site 4f (24 October 1985) using a scanning electron microscope (SEM) equipped with automated X-ray analysis (Johnson et al. 1981). Sediment P was measured by the technique of Sagher (1976). Organic matter content was determined by weight loss of dried samples at 500°C in a muffle furnace. Size fractionation of sediments was performed by sieving fresh samples through 2-mm mesh, drying at 80°C, and then sieving through 1.10-, 0.55-, and 0.25-mm mesh. Size fractions were expressed as percent of total dry weight. Porewater chemistry was determined to assess how it might influence sediment P dynamics. Porewater was sampled by incubating dialysis sacks just below the sediment surface for 1 wk (Mayer 1976).

Results

Streamwater SRP was highly correlated with EPC at six sites along Hoxie Gorge Creek ($r = 0.979, p < 0.01$) under autumnal conditions of low flow (Fig. 2). SRP was always greater than EPC measured by the standard technique of incubating sediments in phosphate solutions with 400 mg $Ca \cdot L^{-1}$.

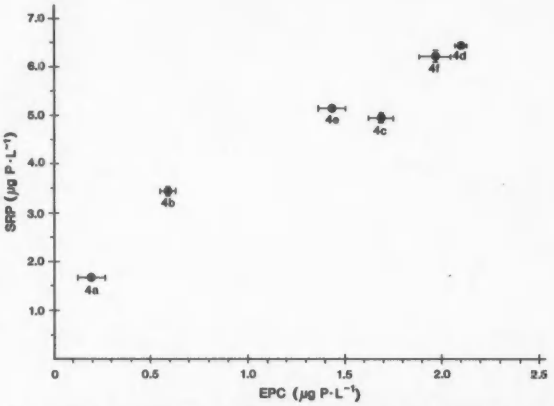

FIG. 2. Mean and SD for soluble reactive phosphorus (SRP) vs. equilibrium P concentration (EPC) for the six Hoxie Gorge sites during low autumnal discharge. Sites 4a and 4b were sampled 21 October 1985; sites 4c–4f were sampled 10 October 1985.

TABLE 1. Effect of Ca on EPC (means (SD)).

Ca (mg $\cdot L^{-1}$)	EPC (μg $\cdot L^{-1}$)	
	Site 4a[a]	Site 4f[b]
0	3.63 (0.16)	29.3 (2.5)
10	1.18 (0.11)	14.6 (1.1)
20	0.85 (0.17)	9.69 (0.27)
30	0.66 (0.25)	7.09 (0.38)
400	0.47 (0.08)	3.91 (0.27)

[a]Sediments collected and analyzed 15 November 1985.
[b]Sediments collected and analyzed 13 November 1985.

The $CaCl_2$ concentration of the solution used for incubation with the sediments during the EPC analyses had a significant effect on the measured EPC. Reducing the $CaCl_2$ concentration to values simulating the Ca levels of the stream significantly increased the measured EPC at both Hoxie Gorge sites 4a and 4f (Table 1). These two sites were chosen because they represented the two extremes in sediment characteristics (see Table 6; Fig. 3). There was a pronounced change in measured EPC in the range of Ca concentrations experienced by the stream. Ca was measured during 1980–81 at site 4f and ranged from 6.6 to 27.5 mg $\cdot L^{-1}$, with a mean of 18.1 ($n = 14$; Klotz 1985). The measured EPC of the sediments at site 4a increased from 0.66 to 1.18 μg $P \cdot L^{-1}$ when Ca was decreased from 30 to 10 mg $\cdot L^{-1}$, while it only increased from 0.47 to 0.66 when Ca was decreased from 400 and 30 mg $\cdot L^{-1}$ (Table 1). At site 4f, measured EPC was 3.91 at a Ca concentration of 400 mg $\cdot L^{-1}$ and increased to 7.09 at 30 mg $Ca \cdot L^{-1}$ and 14.6 at 10 mg $Ca \cdot L^{-1}$ (Table 1). This change in EPC with Ca concentration was due to changes in both phosphate adsorption and desorption (Table 2). Ca concentrations along Hoxie Gorge Creek in October and November 1985 measured 14.6 mg $\cdot L^{-1}$ at site 4a ($n = 1$), 15.4 at 4d ($n = 1$), and 21.6 (2.4) at 4f (mean (SD); $n = 5$).

To determine if P precipitation with Ca could account for the lower measured EPC values at the higher Ca concentrations, phosphate solutions of 25 μg $\cdot L^{-1}$ were incubated with $CaCl_2$

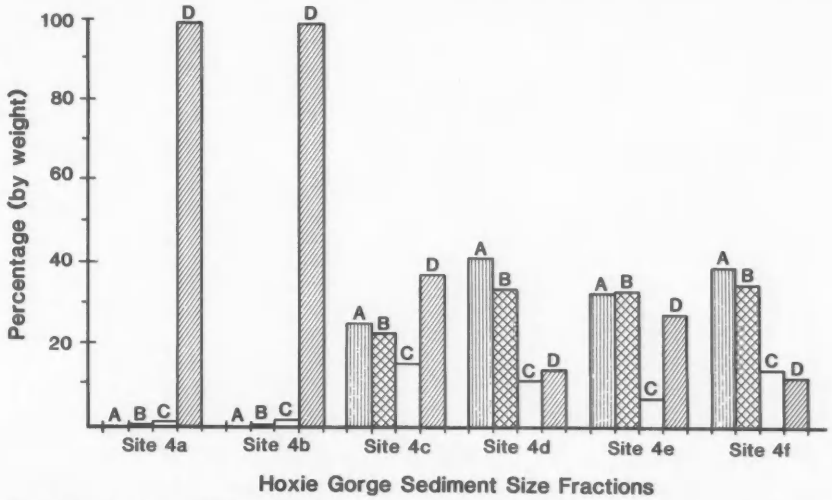

FIG. 3. Size fractions of sediment passing through a 2-mm mesh at the six sites as percentage of total dry weight (collected 24 October 1985). A, 1.10–2.0 mm; B, 0.55–1.10 mm; C, 0.25–0.55 mm; D, <0.25 mm.

TABLE 2. Sorption and desorption of P vs. Ca. Values are μg P·g^{-1} sediment (SD) sorbed (+) or desorbed (−) during 1-h incubation.

Ca (mg·L^{-1})	Initial P (μg·L^{-1})	Site 4a	Site 4f
0	0	−0.421 (0.039)	−0.195 (0.030)
	25	2.36 (0.01)	−0.033 (0.003)
10	0	−0.138 (0.026)	−0.147 (0.017)
	25	2.56 (0.01)	0.083 (0.004)
20	0	−0.101 (0.026)	−0.099 (0.010)
	25	2.59 (0.04)	0.153 (0.001)
30	0	−0.028[a]	−0.080 (0.007)
	25	2.63 (0.03)	0.202 (0.022)

[a]One replicate only.

TABLE 3. Effect of NaCl vs. $CaCl_2$ on EPC (means (SD)).

Solution	Ionic strength (M)	EPC (μg·L^{-1})
RO water[a]	0	13.4 (0.66)
0.375 mM $CaCl_2$	0.00113	6.39 (0.33)
0.750 mM $CaCl_2$	0.00225	4.55 (0.29)
10.00 mM $CaCl_2$	0.03000	2.46 (0.09)
0.565 mM NaCl	0.00057	10.1 (0.44)
1.300 mM NaCl	0.00130	9.53 (0.18)
15.10 mM NaCl	0.01510	6.82 (0.20)

[a]Water purified by reverse osmosis and deionization.

concentrations of 0, 15, 30, and 400 mg Ca·L^{-1}. There were no significant differences in final SRP between the 0 Ca solutions and each of the Ca amended solutions.

When NaCl was substituted for $CaCl_2$ to test the influence of the specific cation, EPC decreased as both NaCl and $CaCl_2$ concentrations increased, but the EPC determined in $CaCl_2$ solutions was lower than that in NaCl solutions at a given ionic strength (Table 3). EPC was not affected significantly by temperature, addition of Al and Fe to the solution, or incubation time (Table 4). Air drying site 4f sediments prior to incubation in 20 mg Ca·L^{-1} solution significantly increased measured EPC to 20.7 from 10.8 μg P·L^{-1} for fresh sediments (Table 4). The ratio of sediment to solution did not significantly alter the measured EPC when incubated in 50 mL of 20 mg Ca·L^{-1} solution. At sediment volumes (site 4f; 8 November 1985) of 0.5, 1.0, 3.0, and 6.0 mL, EPC values (mean (SD)) were 6.43 (0.75), 6.92 (0.33), 6.53 (0.67), and 7.00 (0.26) μg·L^{-1}.

The effect of solution pH on Hoxie Gorge sediments (sites 4a and 4f) was to increase EPC (Fig. 4) and decrease the P sorption index (Fig. 5) at both the acidic and basic extremes,

TABLE 4. Effect of equilibration conditions on EPC. Values are means ± SD for site 4f sediments on 21 October 1985 for temperature experiment, 8 November 1985 for 2.25-h incubation, 4 November 1985 for dried sediments, and 14 January 1986 for Fe- and Al-amended solution.

Experimental condition[a]	Experimental EPC (μg·L^{-1})	Control EPC[b] (μg·L^{-1})
Temperature effect		
0°C	1.61 ± 0.15	2.30 ± 0.17
10°C	2.33 ± 0.11	2.30 ± 0.17
2.25-h incubation	7.07 ± 0.36	6.53 ± 0.67
Dried sediments	20.7 ± 3.47[c]	10.8 ± 0.57
Fe and Al amended[d]	3.78 ± 0.23	5.55 ± 0.76

[a]Temperature effect experiment was incubated in 10 mM $CaCl_2$ solution; the rest were incubated in 0.5 mM $CaCl_2$ solution.

[b]Control EPC was conducted at 20°C for 1 h at $CaCl_2$ concentration of experimental EPC.

[c]Significantly different than control at 0.05 level.

[d]Al added as $AlK(SO_4)_2$ at 0.13 mg Al·L^{-1}; Fe added as $FeCl_3$ at 0.038 mg Fe·L^{-1}. Concentrations used represent those measured in water at site 4f on 20 December 1985.

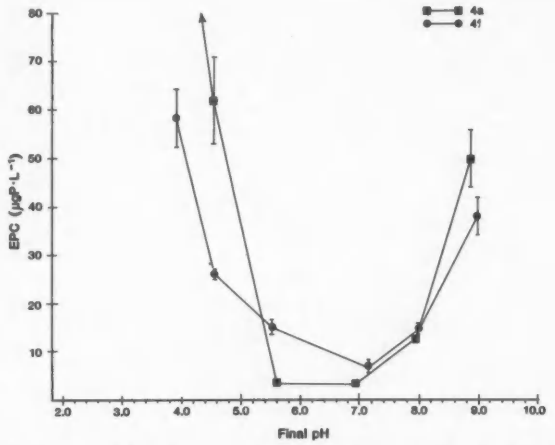

FIG. 4. Equilibrium P concentrations (EPC) vs. pH for site 4a (27 February 1986; 20 mg Ca·L^{-1} solution; 1 mL of sediments) and site 4f (5 February 1986; 20 mg Ca·L^{-1} solution; 3 mL of sediments).

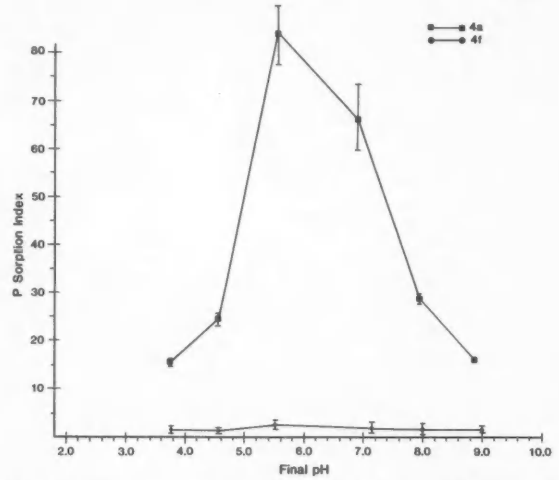

FIG. 5. Phosphorus sorption index vs. pH for site 4a (27 February 1986; 20 mg Ca·L^{-1} solution; 1 mL of sediments) and site 4f (5 February 1986; 20 mg Ca·L^{-1} solution; 3 mL of sediments). Initial P was 2000 μg·L^{-1}.

with EPC at a minimum and the P sorption index at a maximum at a slightly acid to neutral pH. The pH of stream water was 6.9 at site 4a and 7.4 at site 4f on the date of collection of sediments for the pH experiments.

The porewater of stream surface sediments (Table 5) differed geochemically from the water column slightly at site 4f with its porous, coarse-grained sediments and more distinctly at site 4a with its firmly packed, fine-grained sediments (Fig. 3).

Sediment characteristics at the six sites considered potentially important in regulating EPC are presented in Table 6, with sediment size distributions in Fig. 3. EPC (Table 7) was negatively correlated with sediment organic and P content, exchangeable Al, and the P sorption index. EPC was also negatively correlated with the proportion of the finest grain size sediment fraction and was positively correlated with the proportion of each of the next three coarse grain sizes; thus EPC was positively correlated with sediment grain size. EPC was not significantly correlated with exchangeable Fe, extractable Al, Fe, or Ca, or carbonate.

The P sorption index (Table 7) was positively correlated with sediment organic and P content and with exchangeable Al and Fe. The index was positively correlated with the proportion of the finest grain size sediment fraction and was negatively correlated with the proportion of each of the next three coarse grain sizes; thus the P sorption index was negatively correlated with sediment grain size. Site 4a sediments had a much greater ability to sorb large quantities of P and therefore maintain lower solution P concentrations than site 4f sediments (Fig. 6), as was also demonstrated by the difference in the P sorption index values for the two sites (Table 6).

Particle analysis of 4f sediments by SEM revealed that 92.8% of the particles contained some Si X-ray counts, 62.0% some Al, 35.9% some Fe, 18.3% some K, and 3.2% some Ca.

Autoclaving sediments increased measured EPC at both sites 4b and 4f, and EPC at 4b was lower than at 4f for sediments that were autoclaved as well as not autoclaved (Table 8).

Discussion

The significant positive correlation found between EPC and streamwater SRP (Fig. 2) indicates that sediments may be important in regulating SRP concentration. However, a positive correlation between EPC and SRP does not by itself prove that sediments actually control streamwater SRP. To conclude that such a cause and effect relationship exists, knowledge of the mechanism for EPC is essential. In this section I will describe how the P dynamics exhibited by Hoxie Gorge Creek sediments can be explained by a model of P sorption by exchangeable Al that was developed and tested in soils.

The P sorption model incorporates aspects of both the soil solution and the soil itself. Wild (1953) found that exchangeable cations affect the formation of basic Al phosphate and suggested that a possible cause was that cations determine the amount of reactive Al. Coleman et al. (1960) elucidated a mechanism for phosphate reaction with an Al-saturated mont-

TABLE 5. Physical and chemical characteristics of porewater vs. stream water.

	Site 4a		Site 4f	
Characteristic	Porewater	Stream water	Porewater	Streamwater
Ca (mg·L^{-1})	13.9	9.1	9.75 ± 0.07	10.2
Conductivity (μmho·cm^{-1})	72	39	60.5 ± 0.7	41
SRP (μg·L^{-1})	2.5	4.4	4.1 ± 0.0	3.2
pH	6.86	6.75	6.97 ± 0.02	6.96
Alkalinity (mg $CaCO_3$·L^{-1})	37.3	13.1	16.9 ± 0.6	17.3

TABLE 6. Sediment characteristics of Hoxie Gorge Creek (means (SD)).

Site	EPC ($\mu g \cdot L^{-1}$)	P sorption index ($X/\log_{10}C$)	Sediment P ($\mu g \cdot g^{-1}$)	Organic (%)	Exchangeable Fe ($\mu g \cdot g^{-1}$)	Exchangeable Al ($\mu g \cdot g^{-1}$)	Extractable Fe ($mg \cdot g^{-1}$)	Extractable Al ($mg \cdot g^{-1}$)	Extractable Ca ($mg \cdot g^{-1}$)	Carbonate ($mg \cdot g^{-1}$)
4a	0.19 (0.08)	147 (0)	165 (7)	12.05 (0.64)	35.4 (0)	41.5 (1.9)	19.8 (0.5)	6.26 (0.28)	0.87 (0)	2.96 (0.81)
4b	0.58 (0.04)	107 (30)	163 (2)	10.08 (0.15)	73.3 (0)	44.2 (2.8)	13.2 (0.3)	6.44 (0.04)	0.29 (0.02)	3.03 (0.70)
4c	1.68 (0.06)	5.12 (0.31)	57.2 (1.7)	1.94 (0.30)	0.5 (0.6)	14.4 (2.8)	16.8 (0.5)	4.05 (0.13)	0.15 (0.01)	1.00 (0.27)
4d	2.09 (0.02)	2.85 (0.01)	53.4 (3.7)	2.30 (0.18)	0	11.7 (2.8)	24.7 (0.4)	5.29 (0.17)	0.61 (0.02)	0.72 (0.09)
4e	1.43 (0.07)	4.45 (0.14)	66.0 (0)	3.28 (0.21)	0	14.4 (2.8)	28.3 (0.4)	6.77 (0.11)	0.33 (0.05)	1.00 (0.25)
4f	1.96 (0.09)	2.42 (0.21)	27.0 (2.0)	1.85[b]	0	13.1 (4.7)	24.1 (0.7)	5.09 (0.20)	4.6 (1.6)	15.3 (0.32)

[a]See text.
[b]Only one replicate.

TABLE 7. Correlation coefficients for EPC and P sorption index vs. sediment characteristics.

Sediment characteristic	EPC	P sorption index
Sediment size fractions		
0.25 mm	−0.969[a]	0.959[a]
0.25 – 0.55 mm	0.919[a]	−0.881[b]
0.55 – 1.10 mm	0.934[a]	−0.948[a]
1.10 – 2.00 mm	0.962[a]	−0.940[a]
P sorption index	−0.958[a]	
Sediment P	−0.962[a]	0.962[a]
% organic content	−0.971[a]	0.993[a]
Exchangeable Fe	−0.803	0.825[b]
Exchangeable Al	−0.947[a]	0.967[a]
Extractable Fe	0.522	−0.563
Extractable Al	−0.598	0.507
Extractable Ca	0.348	−0.239
Carbonate	0.239	−0.146

[a]Significant at 0.01 level.
[b]Significant at 0.05 level.

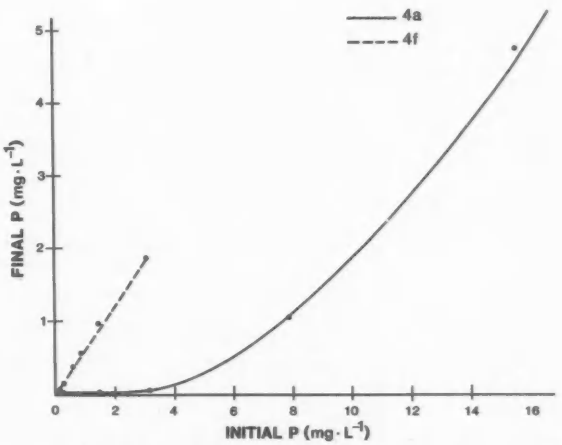

FIG. 6. Final SRP remaining in solution following 1-h incubation vs. initial SRP for site 4a and 4f sediments on 1 April 1986.

TABLE 8. Effect of autoclaving sediments on EPC ($\mu g \cdot L^{-1}$, means (SD)).

Site	Autoclaved	Not autoclaved	Autoclaved/ not autoclaved
4b	8.12 (0.03)	3.94 (0.28)	2.06
4f	15.5 (1.5)	9.68 (0.65)	1.61
4f/4b	1.91	2.46	

morillonite clay in the presence of NaCl. This mechanism was supported by experiments on the effects of ionic strength, Ca^{2+} concentration, and pH on an Al-saturated cation exchange resin (Robarge and Corey 1979) and in an acidic, montmorillonitic soil (Traina et al. 1986a). Others also showed that the rate of phosphate desorption from soil was inversely related to the Ca concentration of the solution (Barrow and Shaw 1979) and adsorption was directly related to Ca (Barrow 1972). A generalized form of the equation of Coleman et al. (1960) given by Traina et al. (1986a) to include the effects of ionic strength and Ca^{2+} concentration is

$$(1)\quad AlX_3\,(s) + (3/n)M^{n+}\,(aq) + H_2PO_4\,(aq) + 2H_2O\,(l) \underset{\longleftarrow}{MCl_n} (3/n)MX_n\,(s) + Al(OH)_2H_2PO_4\,(s) + 2H^+(aq)$$

where X refers to 1 mol of montmorillonite surface charge and M^{n+} is a metal cation, with MCl_n its chloride salt. Equation (1) shows that the ionic strength and metal cation charge of the solution are important in determining the ultimate amount of hydrolyzed, exchangeable Al(III) which can react with phosphate to form $Al(OH)_2H_2PO_4(s)$. Perrott et al. (1974) showed that hydroxy-Al species were readily adsorbed onto negatively charged surfaces where they adsorbed phosphate. The evidence that indicates this mechanism is at work in Hoxie Gorge Creek comes from sorption experiments in which a number of parameters of the incubating solution are varied and from analyses of the sediments.

Sorption Experiments

EPC experiments with Hoxie Gorge Creek sediments are consistent with equation (1). As the ionic strength of the equilibrating solution was increased using $CaCl_2$ (Tables 1 and 3) or NaCl (Table 3), EPC decreased. Also, EPC decreased more rapidly relative to ionic strength in Ca^{2+} solutions compared with Na^+ solutions (Table 3). This result is consistent with equation (1) because a divalent cation should more effectively displace exchangeable Al(III) than a monovalent cation, resulting in more $Al(OH)_2H_2PO_4$ formed and less phosphate in solution, as shown by Robarge and Corey (1979) and Traina et al. (1986a).

The pH experiments with Hoxie Gorge sediments (Fig. 4 and 5) were consistent with equation (1) and the data of Robarge and Corey (1979) which verified the mechanism. Robarge and Corey (1979) showed that as the pH of the solution increases from a low value, adsorption of phosphate becomes greater (EPC decreases) due to increasing hydroxy-Al species. However, at pH values greater than the pH of minimum EPC (maximum adsorption), there is increased competition from hydroxyl ions for adsorption sites (Robarge and Corey 1979); thus, EPC increases because less P is sorbed. The results of my study show that for sites 4a and 4f, EPC is at a minimum at about the natural pH of the stream water. Similar results were also reported in sediment sorption studies by Schofield (1968) and Meyer (1979). Site 4a, with its greater reservoir of bound phosphate (Table 6), showed greater desorption of phosphate at the pH extremes than did site 4f. However, the EPC for 4a was lower than 4f at the natural pH of the stream water. The pH of the equilibrating solution was not a factor in the other EPC measurements of this study, since the pH was found to adjust to the natural stream pH within seconds after addition of the sediments.

The loss of P from solution in the EPC analyses was due to sorption of P by the sediments and not precipitation of P from solution with chemical species added to the equilibrating solution. There was no significant decrease in P as Ca increased in the experiment testing for Ca precipitation from solution, indicating that this mechanism was not responsible for the inverse relationship between EPC and Ca. For comparison, final P concentration (initial 25 $\mu g \cdot L^{-1}$) decreased from 17.5 to 3.5 $\mu g \cdot L^{-1}$ as Ca in solution increased from 0 to 400 $mg \cdot L^{-1}$ in EPC measurements at different Ca levels with site 4f sediments (Table 3). Addition of Fe and Al at natural stream levels to the equilibrating solution did not significantly affect EPC values. Stumm and Morgan (1970) and Meyer (1979) noted that precipitation of iron and aluminum phosphates in solution will not decrease the P concentration below 25 or 100 $\mu g \cdot L^{-1}$; this is higher than the normal SRP of the stream water and P concentrations used in the EPC equilibrations of my study. Meyer (1979) concluded that the low dissolved P in Bear Brook is maintained by sorption by sediments, not precipitation from the water column. Schofield (1968) concluded that Fe and Al additions to solutions used in laboratory studies of Adirondack lake sediments increased P fixation by Fe and Al in the sediments.

Sediment Characteristics and EPC

The data from this study indicate that downstream changes in sediment characteristics in Hoxie Gorge Creek (Table 6; Fig. 3) led to increased EPC and a corresponding increase in streamwater SRP (Fig. 2). EPC was negatively correlated with exchangeable Al (Table 7), as predicted by equation (1); the more exchangeable Al, the more P removed from solution. EPC was positively correlated with sediment size (Table 7), probably because the finer grained sediments have greater cation exchange capacity (Foth 1984), resulting in more exchangeable Al and Fe and greater P binding at the upstream sites (Table 6). The lack of significant correlations between EPC and exchangeable Fe, extractable Al, Fe, and Ca, and carbonate (Table 7) indicates that these species probably did not play a major role in EPC differences between Hoxie Gorge sites. Major geochemical differences in sediment type were not a factor in the downstream increase in EPC, since X-ray diffraction analyses of sites 4a and 4f showed no discernable differences.

Previous studies shed some light on the specific mechanism for the downstream EPC increase in Hoxie Gorge Creek. EPC has been shown to increase as coverage of binding sites by phosphate increases (White and Taylor 1977; Robarge and Corey 1979). The upstream sites at Hoxie Gorge have a greater ability to sorb large quantities of phosphate from solution (Fig. 6), as shown by their much higher P sorption index values; the fine-grained sediments upstream have a higher concentration of P-binding sites than the coarse downstream sediments. The EPC may be lower in Hoxie Gorge for the fine-grained sediments upstream due to their much greater concentration of surface binding sites, and thus their lower percent coverage. It is interesting and important to note that the upstream sediments have lower EPC values and higher P sorption index values than the downstream sites, despite having much higher sediment P values (Table 6). A relationship similar to the negative correlation between EPC and the P sorption index (Table 7) was also found for lake sediments (Macpherson et al. 1958).

Several lines of reasoning indicate that geochemical processes are more important than biological processes in determining the EPC differences between Hoxie Gorge sites. Killing microbes associated with the sediments by autoclaving did not eliminate the difference in EPC between sites 4b and 4f (Table 8). EPC increased for both sites following autoclaving, but the change was greater for 4b than 4f, indicating that there may have been slightly more biological effect on EPC at 4b than 4f. Data obtained from autoclaving experiments are difficult to interpret conclusively due to the potential for physical and chemical as well as biological change caused by the heat and pressure. Other data supporting the importance of geochemical processes in controlling EPC include the fact that EPC did not change significantly with an increase in temperature that would have been expected to increase biological uptake (Table 4). Meyer (1979) also found that EPC varied little with temperature for Bear Brook sediments. Also, the effects on EPC of the cation species and concentration in the equilibration solution (Tables 1 and 3) indicate geochemical processes.

Improved EPC Technique

The results of this study show that the validity of existing EPC techniques can be improved by proper preparation of the equilibration solution and sediments. The equilibration solution should mimic the natural water in terms of ionic strength, specific cation, and pH if valid conclusions are to be made when comparing EPC and water column SRP. The use of unnaturally high Ca levels in the equilibration solution can be traced to White and Beckett (1964), who developed the method for English agricultural soils. They were concerned with a soil water system which would have a substantially higher ionic strength than stream water or porewater in the surface sediments

(Table 5). Mortimer (1949), in an early review, pointed out the significant differences between soils and aquatic sediments. A Ca concentration of 20 $mg \cdot L^{-1}$ was determined to be appropriate for Hoxie Gorge based on water column Ca measurements (Klotz 1985), although Ca varies temporally and spatially. The technique of measuring EPC at natural levels of Ca was validated by incubating 0.5, 1.0, 3.0, and 6.0 mL of sediments in 50 mL of solution to determine if the sediment volume affected measured EPC. The results show that the sediment volume did not affect EPC, a finding similar to Taylor and Kunishi (1971) in their validation of the technique using 400 mg $Ca \cdot L^{-1}$.

Fresh sediments should be used for EPC measurements because dried sediments give significantly higher results. The EPC of dried subsamples from site 4f sediments was nearly twice that of fresh subsamples (Table 4). Twinch (1987) found that EPC increased by a factor of 3 when sediments from a hypertrophic reservoir were dried. Literature EPC values obtained using dried sediments (Taylor and Kunishi 1971; Mayer and Gloss 1980) are probably too high.

While the accuracy of EPC measurements can be greatly improved by using an appropriate equilibration solution and fresh sediments, it would be prohibitively difficult to utilize a synthetic equilibration solution for EPC experiments that exactly duplicated the stream water or porewater on the day of analysis because factors such as organic content (Traina et al. 1986b), specific cations, and pH (Robarge and Corey 1979; Traina et al. 1986a) of the solution all influence EPC. Therefore, one should be cautious in drawing conclusions based on specific comparisons between EPC values measured in the laboratory and water column SRP concentrations.

Role of Sediments in Streamwater Quality

The downstream increase in SRP in Hoxie Gorge Creek may be great enough to influence nutrient limitation. Bothwell (1985) found significant decreases in P limitation as SRP increased from 0.7 to 1.1 and 3.4 $\mu g \cdot L^{-1}$ at three stream sites. The SRP range in Hoxie Gorge Creek (Table 2) was greater than the range in Bothwell's (1985) study, indicating that natural sediment processes may determine nutrient limitation.

The important role played by sediments in regulating SRP should be incorporated into stream management practices. Stream channelization and snag removal lead to increased water flow and a subsequent decrease in the ratio of fine- to coarse-grained sediments. This change would be expected to lead to increased streamwater SRP due to increased EPC. The ability of Hoxie Gorge sediments to buffer anthropogenic P inputs varies with sediment type, as shown by the P sorption index correlations (Table 7). While sediments from all sites were able to remove excess P from solution, the fine-grained sediments from upstream sites had the greatest capacity for removing excess P from the water, despite their already high P content (Table 6). This study provides information which can be used to predict the ability of stream sediments to maintain relatively low streamwater SRP at a given anthropogenic input level. Obviously stream sediments do not provide a limitless sink for P, and therefore the renewal of sorption sites is important for maintaining low SRP values. Renewal is accomplished by high discharge events which wash out stream-bed sediments and bring in fresh sediments from the stream banks (Meyer 1979).

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NOTES

Evidence of Introgressive Hybridization in the Genus *Stizostedion*: Interspecific Transfer of Mitochondrial DNA between Sauger and Walleye

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Billington, N., P. D. N. Hebert, and R. D. Ward. 1988. Evidence of introgressive hybridization in the genus *Stizostedion*: interspecific transfer of mitochondrial DNA between sauger and walleye. Can. J. Fish. Aquat. Sci. 45: 2035–2041.

The mitochondrial genotypes of walleye (*Stizostedion vitreum*) and sauger (*Stizostedion canadense*) are readily differentiated, permitting an analysis of the incidence of hybridization between the taxa. We provide evidence that introgression of sauger into walleye has occurred: two female walleye collected from Lake Simcoe contained a mitochondrial genome identical to that of sauger. Not only were these two fish morphologically indistinguishable from typical walleye, they were homozygous for the diagnostic alleles characteristic of walleye at the *Mdh-3* and *Pgm-1* allozyme loci. Sauger have not been recorded in Lake Simcoe, but a few individuals may have been inadvertently introduced during stocking programs and introgressed with walleye due to a lack of conspecific mates.

Les génotypes mitochondriens du doré jaune (*Stizostedion vitreum*) et du doré noir (*Stizostedion canadense*) sont nettement différenciés et permettent donc une analyse de l'incidence de l'hybridation entre les taxons. Les auteurs présentent des indices d'une introgression du doré noir chez le doré jaune : deux femelles de doré jaune capturées dans le lac Simcoe présentaient un génome mitochondrien identique à celui du doré noir. Non seulement ces deux poissons étaient-ils aussi homozygotes pour les allèles caractéristiques de l'identification du doré jaune au locus d'allozyme *Mdh-3* et *Pgm-1*. Le doré noir n'a pas été signalé dans le lac Simcoe, mais quelques individus ont pu y être introduits par inadvertance au cours d'ensemencements et il est possible qu'ils se soient introgressés avec des dorés jaunes étant donné l'absence d'individus de même espèce au moment du frai.

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While hybridization between species is rare in the animal kingdom (Mayr 1963), introgression, the incorporation of genes of one species into the gene complex of another species, is even less common. The lack of introgression may be a consequence of either hybrid sterility or of isolating mechanisms which prevent backcrossing of fertile hybrids with one of their parent species. Cytoplasmic (e.g. mitochondrial) genomes, which are maternally inherited (Hutchinson et al. 1974; Gyllensten et al. 1985), provide unique markers for the study of introgression (Ferris et al. 1983; Avise and Saunders 1984; Avise et al. 1984a; Campton 1987). Selection on nuclear genomes does not strongly affect the dynamics of extranuclear genomes because of their independent segregation. Modelling studies have shown that such genomes are likely to introgress unless hybrids have very low fitnesses (Takahata and Slatkin 1984; Takahata 1985). There are a rapidly growing number of examples of mitochondrial DNA exchange among taxa (Table 1). In several cases allozyme studies have confirmed that mitochondrial DNA (mtDNA) exchange has not been accompanied by introgression of nuclear genes. This evidence of transmission of mtDNA across species barriers further indicates that nucleocytoplasmic incompatibility plays only a minor role in the reproductive isolation of species.

As a group, fish show rather high levels of interspecific hybridization apparently associated with their employment of external fertilization (Mayr 1963). However, hybridization seems to be considerably more common among freshwater than marine fish. This difference has been attributed to the recency of most freshwater habitats (Hubbs 1955; Mayr 1963; Campton 1987). For example, many freshwater fish species in the Northern Hemisphere have evolved during the Pleistocene, and in these species, isolating mechanisms may have not completely developed. Despite the abundance of reports concerning hybridization among fish species, there are no reports of inter-

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TABLE 1. Records of mtDNA exchange between animal species.

Species and direction	References
Laboratory strains	
Mus domesticus into *M. musculus*	Ferris et al. 1982
Mus domesticus into *M. molossius*	
Natural populations	
Drosophila persimilis into *D. pseudoobscura*	Powell 1983
D. pseudoobscura into *D. persimilis*	
D. simulans into *D. mauritiana*	Solignac and Monnerot 1986
Gryllus pennsylvanicus into *G. firmus*	Harrison et al. 1987
Mytilus edulis into *M. galloprovincialis*	Skibinski 1985; Edwards and Skibinski 1987
Rana lessonae into *R. ridibunda*	Spolsky and Uzzell 1984
Hyla gratiosa into *H. cinerea*	Lamb and Avise 1986
Cnemidophorus gularis into *C. laredoensis*	Wright et al. 1983
Mus domesticus into *M. musculus*	Ferris et al. 1983; Gyllensten and Wilson 1987
Clethrionomys rutilus into *C. glareolus*	Tegelstrom 1987
Odocoileus virginianus into *O. hemionus*	Carr et al. 1986

TABLE 2. Fragment sizes (kilobase pairs) of sauger mtDNA for those restriction endonucleases cutting more than once. Total length of molecule as determined for each enzyme is also shown.

Enzyme	Fragment size	Total length[a]
Apa I	9.02, 5.97, 1.85	16.84
Ava I	5.33, 3.03, 2.90, 2.13, 1.21, 1.02, 0.98, 0.32	16.91
Bam HI	9.71, 3.93, 3.22	16.86
Bcl I	8.15, 6.40, 2.34	16.89
Dra I	8.96, 5.63, 2.22	16.81
Eco RV	8.87, 5.01, 2.10, 0.56, 0.11	16.65
Hind III	9.91, 1.80, 1.70, 1.23, 1.12, 0.98	16.74
Mlu I	13.49, 3.18	16.67
Nco I	16.06, 0.55	16.61
Pst I	8.65, 8.15	16.80
Sca I	8.54, 4.11, 3.06, 1.39	17.10
Sst II	13.39, 1.75, 1.44, 0.26	16.84
Xba I	4.79, 4.60, 2.69, 2.65, 1.33, 0.66	16.72
Xho I	8.45, 8.20	16.65

[a]Mean length = 16.760 ± 0.130 (± SD) (n = 14).

specific mtDNA exchange (Campton 1987). Avise et al. (1984a) reported mtDNA exchange between two subspecies of bluegill sunfish (*Lepomis macrochirus*), but a subsequent study failed to reveal mitochondrial exchange among *Lepomis* species (Avise and Saunders 1984).

The present study provides evidence of introgressive hybridization between two members of the percid genus *Stizotedion*, with the transmission of mtDNA from the sauger (*S. canadense*) into the walleye (*S. vitreum*). Walleye and sauger have similar distributions in North America and occur sympatrically in many water bodies (Scott and Crossman 1973; Trautman 1981). The species are known to hybridize both naturally

TABLE 3. Number of fragments produced in walleye and sauger mtDNA with 24 restriction endonucleases. Walleye data from Billington and Hebert (1988) and sauger data from Table 2.

Enzyme	Walleye	Sauger
Apa I	3	3[a]
Ava I	13	8
Bam HI	2	3
Bcl I	4	3
Bgl II	0	1
Bst EII	1 or 2	1
Cla I	0	0
Dra I	2, 3, or 4	3
Eco RI	1	1
Eco RV	4	5
Hind III	5	6
Kpn I	1	1
Mlu I	1	2
Nco I	3 or 4	2
Pst I	3	2
Pvu I	0	0
Pvu II	1	0
Sal I	2	1
Sca I	4	4[a]
Sma I	3	1
Sst I	0	1
Sst II	3	4
Xba I	2	6
Xho I	2	2[a]

[a]Different fragment patterns were obtained with these enzymes for the two species.

(Stroud 1948; Clayton et al. 1973; Nelson and Walburg 1977) and under experimental conditions (Nelson et al. 1965; Nelson 1968; Lynch et al. 1982; Hearn 1986). Their F_1 hybrids are sufficiently vigorous that they are used in stocking programs (Lynch et al. 1982; Hearn 1986). Moreover, introgressive hybridization between the two species has been suggested as a mechanism for the decline of sauger populations in lakes such as Lake Erie, where walleye is predominant (Regier et al. 1969).

Methods

Sample collection — One hundred and sixty-two walleye were collected from 10 sites across the Great Lakes basin; details of these sites and the 141 walleye analysed for mtDNA variation are provided in Billington and Hebert (1988). Included in these samples were 12 female walleye collected from Lake Simcoe in April 1986 during their spawning run into the Talbot River. In addition, four sauger were collected, three from the central Great Lakes (one from Lake St. Clair (SCS1) and two from the western basin of Lake Erie (ERS1, ERS2)) and one from Issett Lake (ISS1) in northern Manitoba. mtDNA was extracted and purified from 4–5 g of liver tissue by the procedure of Billington and Hebert (1988). Heads were frozen at −40°C and retained for allozyme electrophoretic analysis.

Morphological analysis — Fork length (centimetres) and weight (grams) were measured for each walleye. Fulton's condition factor (K) (Bagenal and Tesch 1978) for each fish was then calculated using the formula

$$K = \frac{100 \times w}{l^3}$$

where w = weight and l = length. The number of spines on the first dorsal fin and the number of spines and rays on the second dorsal fin of walleyes were also counted.

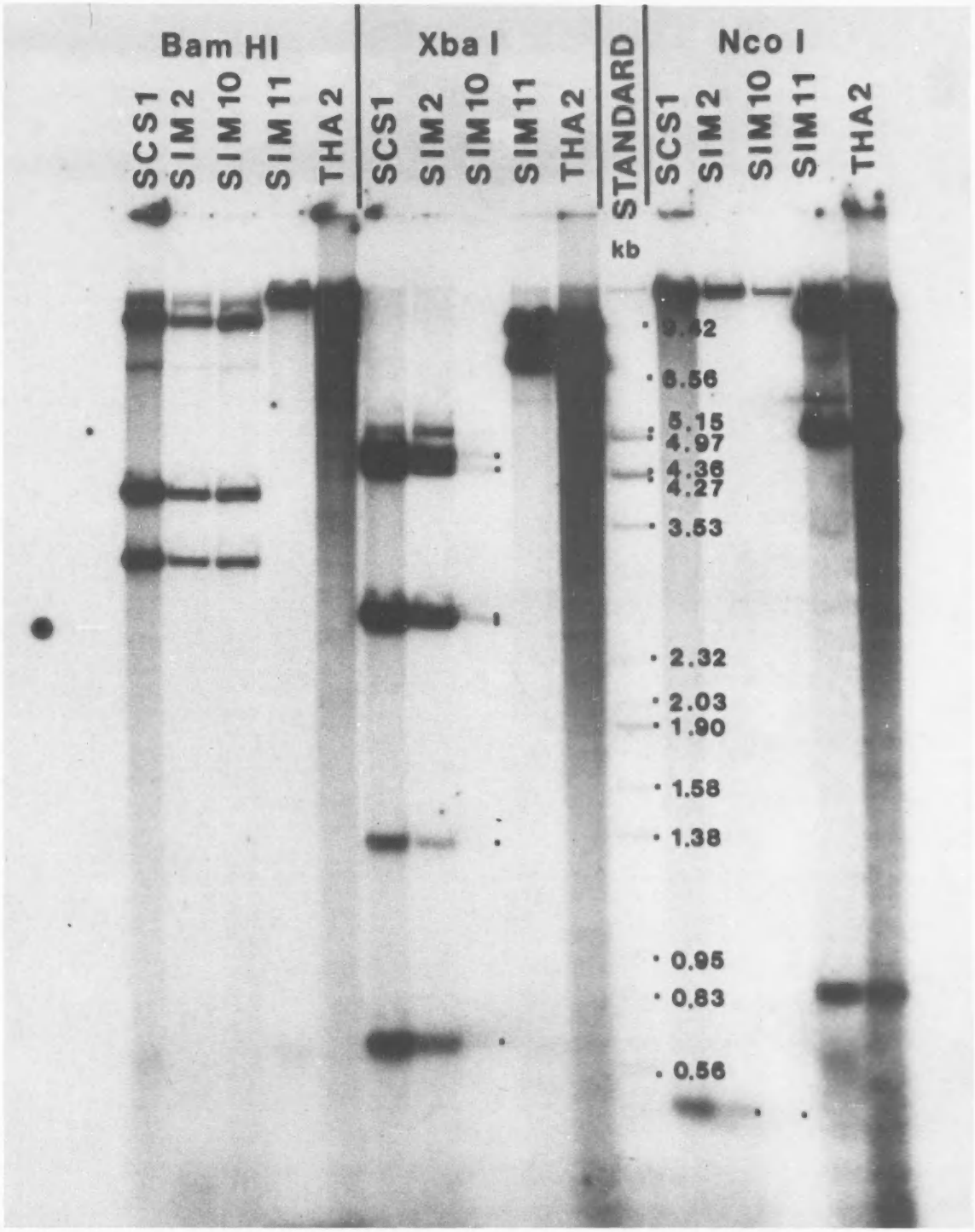

FIG. 1. Autoradiograph (1.2% agarose gel) of mtDNA fragment patterns obtained using the restriction endonucleases *Bam* HI, *Xba* I, and *Nco* I on sauger from Lake St. Clair (SCS1) and walleye from Lake Simcoe (SIM2, SIM10, and SIM11) and the Thames River (THA2). ■ = position of faint bands on gel.

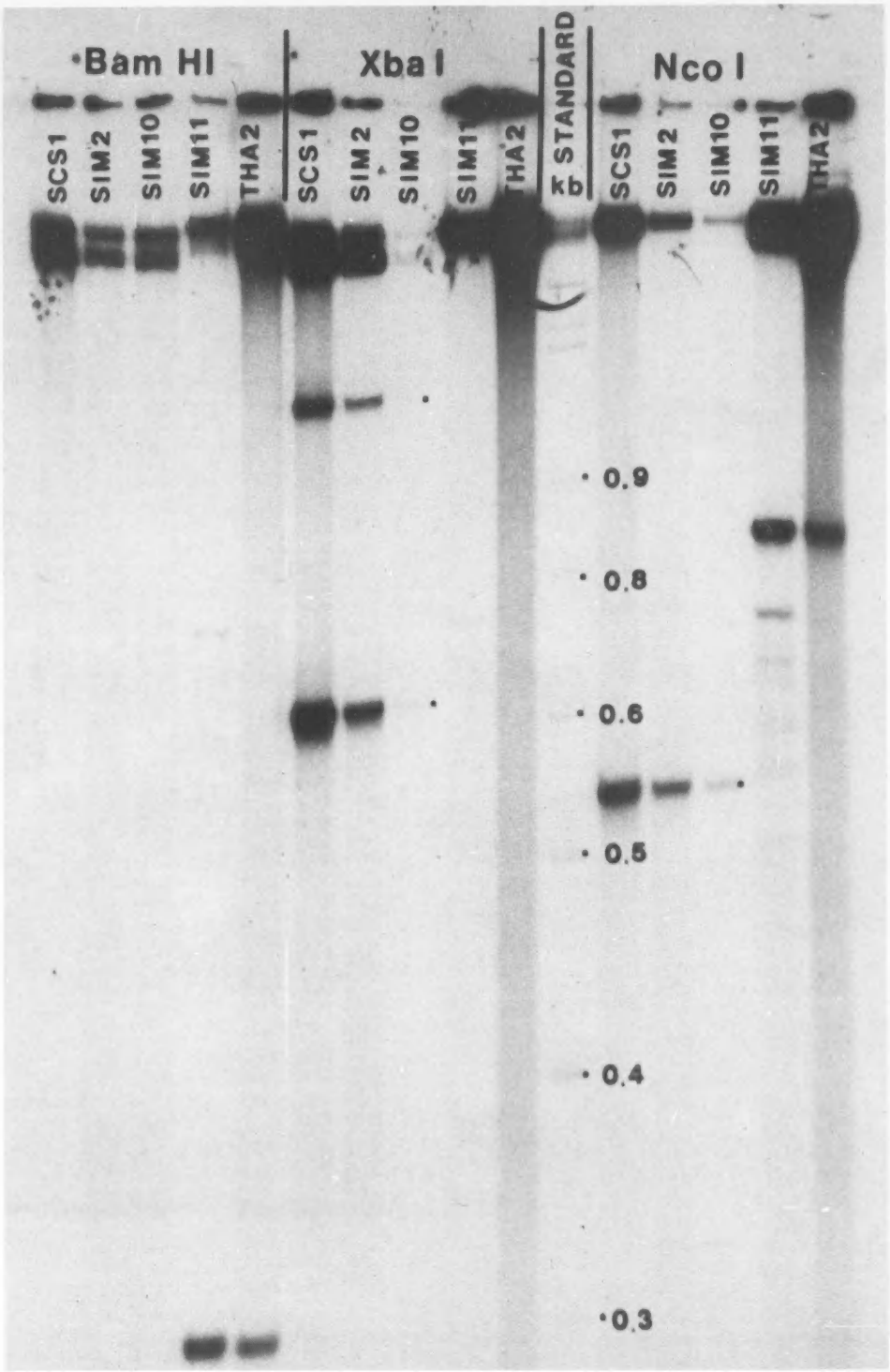

FIG. 2. Autoradiograph (4.0 % acrylamide gel) of mtDNA fragment patterns obtained using the restriction endonucleases *Bam* HI, *Xba* I, and *Nco* I on sauger from Lake St. Clair (SCS1) and walleye from Lake Simcoe (SIM2, SIM10, and SIM11) and the Thames River (THA2). ■ = position of faint bands on gel.

TABLE 4. Morphological data and condition factors (K) for 12 Lake Simcoe walleye, including two fish (SIM2 and SIM10) found to contain sauger mtDNA (t-test: $t_{(10)} = 0.131$, not significant, $p = 0.05$).

Character	SIM2 and SIM10	Other fish
Number of spines on 1st dorsal fin	13–14	13–15
Number of spines and rays on 2nd dorsal fin	1 + 19 1 + 20	1 + 19 (4 fish) 1 + 20 (3 fish) 1 + 21 (1 fish) 2 + 19 (1 fish) 2 + 20 (1 fish)
Mean K	1.250	1.233
Range	1.235–1.265	1.039–1.474

Mitochondrial DNA analysis — mtDNA was obtained from 141 of the 162 walleye and three of the four sauger (SCS1, ERS1, and ISS1). The mtDNA from 67 of these walleye and the three sauger was digested using 24 six-base sequence recognition endonucleases. The mtDNA from the remaining 74 walleye was examined with 10 endonucleases (Billington and Hebert 1988). Details of these endonucleases, including their recognition sequences, and of mtDNA analysis methods are provided by Billington and Hebert (1988).

Allozyme analysis — The genotype of each fish was determined at two allozyme loci (*Mdh-3* and *Pgm-1*), known to be diagnostic between these species (Clayton et al. 1973; T. N. Todd, U.S. Fish and Wildlife Service, Ann Arbor, MI., unpubl. data; R. D. Ward, N. Billington, and P. D. N. Hebert, unpubl. data), using horizontal starch gel (12.5%, Connaught starch) electrophoresis of white muscle tissue. Gels were run at 200 V for 4 h using a continuous Tris–citrate (electrode buffer 0.25 M Tris, 0.057 M citric acid, pH 8.0; gel buffer 1.25 dilution of electrode buffer) buffer system. Stain recipes were modifications of those given by Shaw and Prasad (1970). It should be noted that only three of the sauger (SCS1, ERS1, and ERS2) were analysed for allozymes and that it was not possible to analyse all the walleye for *Pgm-1*.

Results

Restriction fragment patterns of sauger mtDNA — Twenty-one of the 24 endonucleases cut sauger mtDNA at least once; sites were absent for *Cla* I, *Pvu* I, and *Pvu* II. Fourteen of these 21 endonucleases cut sauger mtDNA more than once (Table 2), while the remainder (*Bgl* II, *Bst* EII, *Eco* RI, *Kpn* I, *Sal* I, *Sma* I, and *Sst* I) each produced a single cut. No polymorphisms were found among the three sauger with any of the endonucleases. The length estimate for the sauger mtDNA molecule averaged 16 790 ± 130 base pairs (bp) (Table 2), a value consistent with those of other fish species (Billington and Hebert 1988). Fifty-seven restriction sites (representing 2.04% of the genome) were resolved on the sauger mtDNA molecule with the 24 endonucleases.

Restriction fragment patterns of walleye mtDNA molecule and comparison with sauger — The restriction fragment patterns of walleye mtDNA, obtained using the same 24 endonucleases, are detailed in Billington and Hebert (1988). A comparison of the number of restriction sites obtained for the two species (Table 3) reveals that some endonucleases (e.g. *Ava* I and *Xba* I) show marked differences in the number of cut sites obtained. Furthermore, a comparison of the fragment patterns obtained for sauger mtDNA (Table 2) and walleye (table 2 in Billington and Hebert 1988) shows that the mtDNA of these two *Stizostedion* species may be distinguished using 19 of the 24 restriction endonucleases. Based on a preliminary comparison of restriction site maps of the two species (N. Billington, R. D. Ward, and P. D. N. Hebert, unpubl. data), the maximum likelihood estimate of the number of nucleotide differences per site (d) (Nei et al. 1985) was calculated as 0.720 ± 0.013.

Interspecific transfer of sauger mtDNA into walleye — mtDNA fragment patterns obtained from two of the walleye from Lake Simcoe (SIM2 and SIM10) were identical to those obtained for sauger for all 24 endonucleases; three examples are shown in Fig. 1 and 2. The 10 remaining Lake Simcoe walleye (e.g. SIM11 in Fig. 1 and 2) showed the characteristic walleye patterns for these endonucleases (Billington and Hebert 1988).

Morphologically, all 12 Lake Simcoe fish resembled walleye. All fish possessed the characteristic walleye black spot to the rear of the first dorsal fin and no sauger-like black speckles were observed. Counts of the first dorsal and second dorsal fin spines and rays did not reveal any differences between the two walleyes SIM2 and SIM10 and the other fish (Table 4). Similarly, there were no differences in condition factors (K) calculated for these two fish compared with the other 10 walleye (Table 4).

Electrophoretic analysis revealed that all 12 Lake Simcoe fish were homozygous for the diagnostic walleye alleles at both the *Mdh-3* and *Pgm-1* loci (Table 5).

Discussion

Restriction fragment patterns of sauger and walleye mtDNA were characterized using 24 restriction endonucleases. The mtDNA of these two species was readily distinguished by 19 of these endonucleases, permitting an analysis of hybridization between the taxa. Although intraspecific variation in mtDNA fragment patterns was detected in Great Lakes walleye (Billington and Hebert 1988), no variation was found among sauger mtDNA obtained from the central Great Lakes ($n = 2$) and from northern Manitoba ($n = 1$). The $d = 0.072$ obtained between walleye and sauger is of the same order of magnitude as values reported in other interspecific comparisons of mtDNA divergence between fish species. For example, Thomas et al. (1986) reported $d = 0.025$–0.069 among five (*Oncorynchus* species, a d value of 0.034 was recorded between *Salmo trutta* and *S. gairdneri* (Berg and Ferris 1984), and d ranged from 0.021 to 0.373 between *S. gairdneri* and *S. clarki* (Wilson et al. 1985). Values of d for intraspecific comparisons of mtDNA divergence among nine walleye clones ranged from 0.0015 to 0.0060 (Billington and Hebert 1988), which are comparable with other intraspecific comparisons of fish mtDNA variation (Wilson et al. 1985; Thomas et al. 1986).

Sauger mtDNA was found in two walleye from Lake Simcoe. These two fish were otherwise indistinguishable from walleye on morphological and allozymic criteria. The results suggest that at least one female sauger hybridized with a male walleye, producing viable female offspring. Walleye–sauger hybrids apparently occur infrequently in nature (Stroud 1948; Clayton et al. 1973; Nelson and Walberg 1977) and may be produced experimentally (Nelson et al. 1965; Nelson 1968; Lynch et al. 1982; Hearn 1986). Following the hybridization event, female offspring of the hybrid presumerably backcrossed with male walleye, so that the sauger nuclear genome has become increas-

TABLE 5. Diagnostic allozyme loci between *S. vitreum* and *S. canadense* (sample numbers in parentheses). Great Lakes walleye collected from 10 sites described by Billington and Hebert (1988). Sauger from western Lake Erie (ERS1 and ERS2) and from Lake St. Clair (SCS1).

Allozyme and locus	Allele	Great Lakes		Lake Simcoe
		Walleye	Sauger	Walleye
Malate dehydrogenase (*Mdh*-3)	100	1.00 (150)	—	1.00 (12)
(EC 1.1.1.37)	140	—	1.00 (3)	—
Phosphoglucomutase (*Pgm*-1)	80	0.004	1.00 (3)	—
(EC 2.7.5.1)	100	0.996 (126)	—	1.00 (12)

ingly diluted. In a study involving two mouse species, 95% introgression of the nuclear genome was recorded within 10 generations of serial backcrossing (Gyllensten et al. 1985), yet the mitochondrial genome remained identical to that of the original female parent.

The discovery of sauger mtDNA in walleye from Lake Simcoe is puzzling, as sauger have never been recorded from this site (MacCrimmon and Skobe 1970; Scott and Crossman 1973; T. Rance, OMNR, Sibbald Point Assessment Unit, Lake Simcoe, pers. comm.). However, the Lake Simcoe walleye population was supplemented by stocking between 1921 and 1955 (MacCrimmon and Skobe 1970), with eggs and fry from the St. Lawrence River (T. Rance, pers. comm.), a site at which sauger and walleye not only occur sympatrically (Scott and Crossman 1973; Bergeron and Brousseau 1983) but are thought to introgress (S. Pepin, MacDonald College, McGill University, pers. comm.). The original hybridization event may have occurred prior to stocking, or alternatively, it is possible that some sauger were inadvertently stocked and introgression occurred in Lake Simcoe as a result of a lack of conspecific mates.

The introgressed sauger genomes were identical to those of sauger from Lake St. Clair, western Lake Erie, and northern Manitoba. Moreover, the two walleye containing sauger mtDNA were clearly not F_1 hybrids, since they were not heterozygous at the two loci which distinguish the parent taxa. The fact that both fish were homozygous for the walleye alleles suggests that the hybridization event occurred at least two generations ago. In a recent survey of allozyme variation in Lake Simcoe walleye, a single individual was found to possess the sauger *Mdh-3* allele, but not the *Pgm-1* allele (G. W. Martin and P. E. Ihssen, OMNR, Maple, Ont., pers. comm.), providing further evidence of hybridization and backcrossing of sauger into walleye in this population.

An alternative explanation, that the mtDNA pattern found in SIM2 and SIM10 resulted from stochastic sorting and differential extinction of mtDNA lineages from polymorphic walleye ancestral stock (Avise et al. 1984b, 1987) deserves consideration. For example, the Lake Simcoe walleye population might contain two distantly related mtDNA lineages. However, the mtDNA found in SIM2 and SIM10 produced identical gel profiles to those of sauger mtDNA for all of the 19 endonucleases that showed differences between the walleye and sauger. Moreover, the extent of the sequence divergence between walleye and sauger mtDNA is approximately 7%, a value commensurate with that observed among fish species (see above) and an order of magnitude greater than the maximum intraspecific variation of 0.6% observed in walleye (Billington and Hebert 1988). Thus, it would appear unlikely that walleye and sauger share a lineage that has accumulated no evolutionary mutations as revealed by 19 endonucleases.

Introgressive hybridization has been suggested as the mechanism by which the blue walleye population in Lake Erie became extinct (after the population size was reduced by pollution and overfishing) and has also been implicated as a factor in the decline of the sauger in Lake Erie and Lake St. Clair (Regier et al. 1969). The present study provided no evidence that this mechanism resulted in the loss of Lake Erie sauger. Specifically, in a survey of mtDNA variation in 141 walleye collected at 10 sites across the Great Lakes, no other cases of introgression of sauger into walleye were detected (Billington and Hebert 1988). Similarly, 162 walleye from the same populations (wherever possible, the same individuals) were sampled for allozyme variation. With the exception of one possible backcross individual collected from Lake Erie, no sauger alleles were detected in the walleye. Thus, there seems to be little evidence to support the view that introgressive hybridization was a factor in the decline of Great Lakes sauger populations (Regier et al. 1969).

mtDNA studies may prove valuable in assessing the success of stocking programs employing the progeny of reciprocal crosses between walleye and sauger. For example, Lynch et al. (1982) produced walleye female × sauger male hybrids (designated "saugeye") in order to combine the more rapid growth and larger size of walleye with the ability of sauger to adapt to small impoundments. More recently, Humphreys et al. (1984) stocked reservoirs with both saugeye and the reciprocal hybrids. Humphreys et al. (1984) found it impossible to distinguish the two hybrid classes morphologically, but such discrimination could be readily accomplished on the basis of their mtDNA genotype, which would always be that of the maternal parent. Hearn (1986) showd that F_1 hybrids of sauger females × walleye males were able to backcross to sauger males. He also found that it was possible to produce F_2 fish in the hatchery and that these fish survived for a number of years when stocked in ponds. Whether the F_1 or F_2 hybrids are able to naturally reproduce in the field remains to be seen.

In the light of these attempts to use walleye × sauger hybrids in fisheries management, further genetic studies are required. Used in conjunction with allozyme electrophoresis, mtDNA studies will allow the incidence of hybridization and introgression in the two North American *Stizostedion* species to be thoroughly investigated. For example, it will be possible to use mtDNA as a marker of the maternal species in hybridization studies and to obtain information on the rate and direction of introgression in these species.

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PERSPECTIVES

Salmon Management and the Search for Values[1]

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This perspective addresses the role of human values in North American salmon management. Salmon resources have been aided and harmed by technology, and managers must carefully assess how current and future technologies will be used to manage salmon. Effective managers must be knowledgeable of fishery science and human values. The science in fishery management is the objective, logical, and systematic method of obtaining reliable knowledge about fishery resources. The art in fishery management involves our values, that is, what we judge to be good, desirable, and important in the long run. A rational management plan is a selective embodiment of the values of the manager or of the organization or society that the manager represents. More surveys are needed to assess the values of the public toward salmon resources. Several potentially desirable directions are discussed for future salmon management in the Pacific Northwest.

Le présent article porte sur le rôle des valeurs humaines dans la gestion du saumon en Amérique du Nord. La technologie a aidé et nui à la fois aux saumons, et les gestionnaires doivent évaluer avec beaucoup de soin comment les techniques actuelles et futures seront utilisées en vue de gérer le saumon. Les gestionnaires efficaces doivent connaître l'halieutique et les valeurs humaines. La science dans le domaine de la gestion des pêches constitue la méthode objective, logique et systématique pour obtenir des connaissances fiables sur les ressources halieutiques. Par contre l'art dans ce même domaine touche à nos valeurs, c'est-à-dire ce qui nous semble bon, souhaitable et important en fin de compte. Un plan de gestion rationnel est une personnification sélective des valeurs du gestionnaire, de l'organisme ou de la société qu'il représente. D'autres études sont nécessaires afin d'évaluer les valeurs du public à l'égard du saumon. Plusieurs orientations qui peuvent être souhaitables sont abordées en vue de la gestion du saumon dans le Pacifique nord-ouest dans les prochaines années.

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> The problems of salmon management... represent in microcosm some great issues of our time.
>
> ...many analysts see mankind to be entering a threefold crisis. Firstly... of numbers; secondly... of scarcity; and thirdly, of values (we have lost sight of how we ought to live).
>
> —Mundie 1977
>
> When very little is known about an important subject, the questions people raise are almost invariably ethical. Then, as knowledge grows, they become more concerned with information and amoral, in other words more narrowly intellectual. Finally, as understanding becomes sufficiently complete, the questions turn ethical again. Environmentalism is now passing from the first phase to the second phase, and there is hope that it will proceed directly on to the third.
>
> —Wilson 1984

Science and Technology in Search of Values

The salmons (*Oncorhynchus* sp. and *Salmo salar*) are examples of fish resources simultaneously aided and harmed by advanced human technology. On the positive side, managers of oceanic salmon fisheries off the Pacific coast of North America now establish fishing seasons with the aid of detailed computer programs and spreadsheets that simulate potential harvest patterns and evalute quickly and precisely (although not always accurately) the effects of alternative management strategies on yields, allocations, and escapements (Johnson 1975; Larkin 1979; Wright 1981; Pacific Fishery Management Council 1985). Technological advances in electrofishing (Reynolds 1983), hydroacoustics (Thorne 1983), and radio and ultrasonic telemetry (Winter 1983) have allowed biologists to penetrate the depths of rivers and lakes and learn about many aspects of salmon life histories heretofore hidden from view. Technologies for the artificial propagation of salmon for mitigation, enhancement, or food have also advanced rapidly on several fronts, including nutrition (Leitritz and Lewis 1976), genetics (Hershberger and Iwamoto 1985), rearing facilities (Senn et al. 1984), disease control and treatment (Leong and Barila 1983), stress detection (Barton and Toth 1980), and reproductive physiology (Billiard 1982). Larkin (1980) forsees that twenty-first century salmon managers will use vast new technologies such as genetic engineering and tissue culture for maintenance, mitigation, and enhancement of salmon.

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Nevertheless, at least as many other technological advances have been harmful to salmon or their habitats. Development of large-scale hydropower has prevented or impeded the movement of salmon up most of the world's large salmon rivers (Netboy 1958; Salo and Stober 1977; Blumm 1981). Advances in low-head and small-scale hydropower threaten to block many smaller rivers previously spared from dam construction. Advancing technologies in agriculture, forestry, and mining have enabled humans to alter or destroy salmon habitat much more quickly than in the past, and far more rapidly than the salmon stocks can respond through natural selection. And even hatchery technology, which can be a beneficial tool of salmon management if used wisely, can result in the spread of diseases (Oregon Department of Fish and Wildlife 1982a, 1982b), straying and resultant changes in stock composition (Nicholas et al. 1982), undesired competition between hatchery and wild salmon stocks, and expansion of offshore fisheries to the preclusion of needed escapements of wild stocks (Oregon Department of Fish and Wildlife 1982a, 1982b). The problems created by hatcheries for wild stocks are particularly insidious because other nonfisheries users of water resources such as developers of hydroelectric power frequently pacify the fishery proponents by financing the construction of one or more hatcheries along with their dam. These hatcheries must mitigate for — not militate against — the affected salmon resources. If hatcheries are to benefit salmon rather than harm them, managers must carefully and consciously define if, how, and when the hatcheries are to be used in a comprehensive salmon management plan. The proper role of hatcheries in salmon management is one specific case of two larger, related issues: *Where, when, and what kinds of technologies should be used in salmon management in the twenty-first century and beyond? What is our philosophical basis for using these technologies?* Technology has effectively given us dominion over the salmon. This generation must decide how salmon are to be managed, and how fully salmon should be forced to participate in our technological revolution. Perhaps we sufficiently value natural, untampered ecosystems and the maintenance of wild stocks to insist on in-river harvest and management of these individual wild stocks, by using comparatively benign technologies such as computers, unobtrusive sampling gear, small-scale habitat manipulation, and, where needed, stock-specific hatchery programs. Or maybe such management, however ecologically rational and inexpensive to implement, is mere fantasy in view of our overall technological capabilities as well as the economic and social benefits to specific users. Perhaps the days of the truly wild salmon are behind, and the future of salmon is not ecological but production agricultural, as for domesticated animals such as cows, sheep, or pigs, ranched and pen-reared by humans by the application of diverse high technologies. Perhaps salmon are to be managed in nature's way, based on ecological principles, using appropriate technologies as tools. Or perhaps our aim is really to develop and manage our technologies for their own sakes, using salmon as the tools — as mere raw materials for our technological experiments. We must decide which technologies should be used, and why.

To deal with these issues wisely, managers must understand three diverse considerations: the nature of fishery management, and salmon management in particular; how the salmon management systems evolved; and the personal or societal value system on which the management of salmon is to be based. Rational salmon management is not just a search for technologies: it is a search for values.

In the first of three sections in this perspective, I propose a new definition of fishery management and discuss the relation between science and art in salmon management. Secondly, the role of values for a salmon manager is considered. Thirdly, the roles of technology and values are considered in suggesting possible directions in several aspects of salmon management. Examples are drawn from the Pacific Northwest salmon management systems.

Art, Science, Fishery Management, and the Salmon Manager

According to Bennett (1970), "Fishery management can be defined as the art and science of producing sustained annual crops of wild fish for recreational and commercial uses." Although some salmon managers today might question Bennett's use of the restrictive word *wild*, variations of this definition have been accepted without major discord. In recent years, through the development of the optimum sustainable yield concept (Roedel 1975), managers have become more aware of complex economic and social concerns of fishery management in addition to biological ones. Indeed, in a popular text entitled "Fisheries Management," Nielsen and Lackey (1980) gave no one-sentence definition of fishery management, but instead identified it as diverse activities related to the aquatic biota, the aquatic habitat, and the human users. Definitions like that of Bennett (1970) and generalized statements of complexity like that of Nielsen and Lackey (1980) were often presented by professors to students on the first day of class, and not mentioned again. The coursework consisted almost entirely of scientific and technological approaches to management.

Many incipient salmon managers thus entered the work force with a good education on specific management techniques but less of an education of when, where, and (most important) why to use a particular tool of salmon management. Many of these managers had little time to think about why they were performing specific technical actions; their technological skills progressed ahead of their philosophies. Their way of dealing with the complex, irrational, or illogical aspects of their jobs was usually to rely on what Bennett (1970), Nielsen and Lackey (1980), and others have called the *art* aspect of management.

Art is commonly said to be a large part of fishery management; it was even placed before science in Bennett's (1970) definition. Nielsen and Lackey (1980) wrote: "Indeed, the question of whether fisheries management is an art or a science is a favorite subject of debate for fisheries professionals (professors usually argue that management is science, managers usually argue for art!)." Although technology itself has blurred the distinction between science and art (Grant 1986), a distinction between them can still be made.

The definition of science has of course been long debated, and no universally held definition exists. Lastrucci (1963), after examining many texts and references on the subject, called science "an objective, logical and systematic method of analysis of phenomena, devised to permit the accumulation of reliable knowledge." The key words are objective, logical, and method. Science is a *method* that to the extent possible is free from value judgments. For example, most salmon managers would agree that the quantitative models of stock and recruitment (Ricker 1954), the understanding of the effects of climate (e.g. El Niño) on salmon abundance (Pearcy 1983), and the physiological and behavioral theories of homing (Hasler 1966) and oceanic migra-

tion (Royce et al. 1968) are all parts of the science of salmon management.

Most fishery professionals today have participated in and witnessed the development of fishery science, and have a clearer understanding of science than of art. To some managers, it seems that the art is little more than a breezy way of saying that our scientific knowledge of a particular process or method is incomplete or imperfect. For example, most salmon managers have been told at least once in their careers that interpreting salmon scales is an art, evidently because one must guess at some of the ages of fish that have poorly defined annuli on their scales. By this line of reasoning, interpreting highly confusing scales from old brook trout (*Salvelinus fontinalis*) is even more of an art — even though one probably feels much less like an artist after the tenth consecutive artistic guess.

Fortunately, other salmon managers recognize that art in management consists of more than spinning a roulette wheel, talking fast, or managing by the "seat-of-the-pants" (Healey 1982) when science and technology let us down. The scale example above merely demonstrates inadequately developed science or technology — not art in any important sense. The art of fishery and salmon management involves our values — that is, what we judge to be good, desirable, and important in the long run.

Roubiczek (1969) stated that "a value expresses the *significance*... which man ascribes to matters related to a particular activity or experience or to his life in general and thus *provides him with guidance for his behavior*" (italics added). These values may be developed within a generation, or may persist over many generations.

Rand (1975) defined art as "the selective re-creation of reality according to an artist's metaphysical value-judgments." In her words, by selective re-creation, "art isolates and integrates those aspects of reality which represent man's fundamental view of himself and of existence.... Art is the concretization of metaphysics. Art brings man's concepts to the perceptual level of his consciousness and allows him to grasp them directly, as if they were percepts.... *Art is the voice of our philosophy*" (italics added). Art in its many forms contains what Rand called cognitive abstractions (what is) and normative abstractions (what ought to be) and is a primary medium for communicating our philosophy and our values to others. Just as a motion picture or a novel conveys a sense of the values of the director or novelist, our management of fishery resources conveys the values of the fishery manager, or, in common property fisheries, of the society or constituency that the manager represents. If art is the voice of our philosophy and fishery managers must use art in their management, then clearly fishery managers must work to develop a coherent philosophy to guide their actions.

The management plan and its implementation are the salmon manager's works of art. Unlike a landscape painter, however, salmon managers do not start with a clean canvas. Instead, a manager attempts to reshape nature's artworks — complex communities, populations, and habitats — within physical and biological constraints, according to the values of the manager or those of society.

Since most fishery managers in Western countries equate inaction with laziness, most make changes — few adopt a "do nothing" philosophy. Fishery management thus can be defined analogously as *the selective modification of fish communities, populations, and their habitats, according to the manager's or society's value judgments*. Fish communities and populations and their habitats, and the values of the manager or society, thus are all part of fishery management. The fishery itself is one part of the modification. Unlike Bennett's (1970) definition, this one does not promote a particular goal; management need not be good, by our values, or even be directed toward a specific goal to still be management. But just as Rand (1975) argued that an artist's primary purpose is to "bring his view of man and of existence into reality," a goal-oriented salmon manager's primary purpose is to modify salmon resources consistent with his or society's values of what the resource should provide and how mankind should interact with it. Ironically, fishery managers have consistently underrated and underutilized art in their management — while all the time professing to use it often. They actually use mostly educated guesses, often based little on articulated information about their own values or those of society.

Public values and attitudes can and should be identified, at least approximately, by census-like surveys and questionaires. In the late 1970s, the U.S. Fish and Wildlife Service sponsored survey research on selected attitudes of Americans toward animals and wildlife issues (Kellert 1980). In Kellert's (1980) surveys, an appropriate distinction was made between the general public and special interest groups. Public values and attitudes can then be expressed through government policy statements or administrative rules, such as the Oregon Department of Fish and Wildlife's "Wild Fish Management" Policy (Oregon Department of Fish and Wildlife 1984). This policy, for example, affirms the public's intent to maintain genetic diversity and the associated benefits of wild, naturally produced fish.

Public surveys and the resulting policies are best drafted during periods when no imminent economic or social crises threaten the major special interests. During crises, the longer term values of the public toward salmon resources may be undermined by immediate concerns of vocal special interest groups for next year's harvest or similar demands, expressed either by the interest groups themselves or through elected officials inordinately pressured by them (Wright 1981). Seldom are the long-term values of the public at large sought or recognized explicitly at ad hoc so-called "public" fishery meetings during times of crisis; instead, actions center on appeasing the demands of vociferous, on-site user groups. If no meaningful survey of public values is available and sufficient or adequate policy statements have not been developed for salmon resources, managers may take an intellectual and political shortcut, spare themselves some verbal abuse from special interests, and assume that more fish, however produced, in the short run is automatically better management — regardless of long-term impacts on stocks or ecosystems, loss of future scientific information, or loss of subsequent management options. In such a situation, a salmon hatchery becomes more than a selectively used technological tool of management: it becomes a politically acceptable symbol of more fish (at least potentially) and less shouting, and embodies a simple, easily understood goal of better management: produce more fish through any available technological method. The goal embodies modern agribusiness more than ecology.

Historically, this process has allowed some salmon managers to forego developing a more complex, long-term, ecologically oriented philosophy in favor of a simpler, short-term, production-oriented one. The desirability of living with the ecological or technological ramifications of, for example, mixed-stock oceanic fishing or mega-hatcheries is seldom considered explicitly. Without a clearly defined and expressed value system on which to base management, the intellectual default of managers, supported by special interests and acquiesced to by the

public, has usually been that high-technology salmon management of almost any form is desirable, so long as it can possibly provide more fish and squelch the complaints of the most powerful special interest groups. But any failure to adequately consider art and broad societal values does not diminish their importance in formulating policies for sound management. The art in salmon management reflects our values toward the salmon populations and habitats, toward land, water, and nature in general, and toward ourselves. If in science and technology we find the methods of managing salmon, in art we find the meaning.

Values, the Salmon Manager, and the Management Plan

In a hypothetical simple case, if the owner of a salmon river were also its manager, his management plan for the river and its stock(s) would embody his values. But in a second, more complex, and prevailing case in nearly all economically important fishery resources, including common property, the owners of the resource (e.g. society, an association, or a corporation) and the manager are not the same people. The manager's role is then more complicated. In most instances, the primary role is to manage according to the values of the owner, the owner's association, or society — not just for the manager's own values nor, in common property situations, just for special interests. The manager, who seldom controls the resource itself, must interpret the values of the owner's association or society and express them in the management plan.

One expression of the manager's own values is in his choice of employment. If the values of the manager conflict so much with those of the owners or those of society's managers that he cannot in good conscience prepare or implement the requested form of a management plan, he can seek to manage someplace else where his values and beliefs are not compromised. Fortunately, there are often less drastic options. The manager can also tactfully exchange relevant scientific information and philosophical perspectives on resource use with the owners or the public, either individually or more formally through his management agency. The manager can also inform them of management options and the philosophical motivations and scientific evidence supporting these options. He must also assess, either formally or informally, the values of the owners or public, either through his own studies or by reviewing those of others. His management plan will thereby better match the values of his clients. The manager not only acts as an educator to the owners or public, but is educated by them about their values; he must be a student of not only fishery science, but also of values.

Suppose an individual salmon manager seeks a scientifically rational, congruent, value-oriented management plan for a salmon river and its stocks. He finds an owner, fishery association, or society sharing these values and is hired to create such a plan. Further suppose that the goal of the plan is "preservation of the individual native salmon stocks in that river system and the associated cultural use of those stocks" (a definition proposed by Lichatowich 1985). Once this goal has been articulated, the manager has a basis for stating specific objectives and then tasks to achieve the goal. Such a plan, if effectively implemented, might endure for many years, even centuries, barring catastrophic man-made or natural environmental changes. Two, three, 10, or thousands of people with similar values could be represented by such a plan, even if their values differed, if they could agree on which values were to be expressed in the plan. Just as important, such a plan insures that certain objectives and tasks, such as widespread stock transfers, construction of mixed-stock megahatcheries, and mixed-stock oceanic fisheries would by conscious choice not be implemented. A rational management plan, like other works of art, is *selective* — some management actions are permitted, and some are excluded.

In the Pacific Northwest, however, management has been based more often on an *accumulation*, not a selective integration, of different vaguely defined value systems of inland and oceanic commercial fishers, inland and ocean recreationists, diverse Indian tribes, fish culturists, salmon ranchers, and the public at large. This accumulation is the by-product of complex compromises among the various users. In implementing these accumulated management plans, actions have often been conflicting and contradictory within and between agencies. Management agencies have directed much research and development toward the artificial propagation of salmon for widespread mitigation and enhancement, while other portions of these same management agencies acted to perpetuate the wild stocks of salmon. Much management-sponsored research has been directed toward identifying and characterizing distinct stocks of salmon, while other management has been directed toward not only maintaining, but also institutionalizing, through long-standing salmon commissions and Federal Fishery Management Councils, mixed stock oceanic harvest of these same stocks. Much (although not all) of the feverish activity of one group of managers and the researchers supporting them both between and within agencies has been counterproductive to other such groups.

As an example, consider the Pacific Fishery Management Council's (1984) harvest management objective 3.2.1.1: "Establish ocean harvest rates for commercial and recreational fisheries that are consistent with requirements for optimum spawning escapements, treaty obligations, and continuance of established recreational and commercial fisheries within the contraints of meeting the conservation and allocation objectives." The meaning of this sentence may not be clear after several readings, but it is clear that many pieces of value systems are represented here, not all of which are compatible with each other. There is little of the selectivity in this objective that art in fishery management demands. No major management options are excluded (e.g. wild stock preservation, hatchery development for increased production, oceanic harvest, in-river harvest, commercial fisheries, recreational fisheries). Management of the common property salmon fisheries has created a management commons, where shards of all value systems are expressed, but none are expressed completely. The assumption is evidently that none of these many value systems or management approaches are mutually exclusive, and that if the Council can just hire the right systems modeler, develop more advanced enhancement technologies, and collect more reliable data, most of these obvious philosophical incompatibilities will disappear. In the words of Garrett Hardin (1969): "An implicit and almost universal assumption of discussions published in professional and semi-popular scientific journals is that the problem under discussion has a technical solution." In the example above, it is unlikely that such a solution can be found at all, let alone in the near future.

Similarly, in one of the few papers directly addressing the basis of salmon management, Larkin (1980) supported the merits (genetic and ecological) of stock specific salmon management: "...easing back on harvest rates provides a better base

for what might be called 'across the board' or 'orchestrated' enhancement, which would have as a goal the restoration to natural levels and subsequent maintenance of the maximum number of natural stocks of all species. The management goal might be a rate of harvesting perhaps at a level as low as what we now see as m.s.y., operating on stocks that are twice as abundant and genetically far more fit than they are today.... It's a nice dream." Just three paragraphs later, we read: "I have recently advocated... [the] large scale introduction [of Pacific salmon] on the Atlantic coast of Canada (where it could be expected that there might eventually be formed a Society for the Extermination of Pacific Salmon. By the year 2000 the battle should be well underway.)" Evidently the natural Pacific salmon stocks are worth saving, but less concern is needed for the natural Atlantic salmon stocks in Canada and elsewhere potentially affected through straying, diseases, competition, or increased mixed-stock fishing pressure that such a "successful" introduction would induce.

Unfortunately, many such philosophical incompatibilities are characteristic of the Pacific Northwest salmon management that Larkin (1980) himself called "the most sophisticated in the world." If the simple management plan for a river that we described earlier is a thematically unified artwork, then most Pacific Northwest salmon plans are themeless collages — surrealistic aggregations of incongruent management goals, objectives, and actions suggestive of many value systems but truly indicative of none. Such is the end result of broadly coordinated, painstaking efforts of hundreds of managers and user-groups representing diverse, often incompatible, value systems — some articulated, some not.

In future management plans, we must emphasize and develop methods to better identify and define the value system and formulate truly public policies to guide salmon management. We must also expend more effort to determine whether different value systems and management philosophies can be accommodated at all. Any successes in these areas would improve the quality and lower the cost of salmon management, as well as reduce wasteful or counterproductive human activity undertaken in its behalf.

How do we go about identifying and defining the value systems on which salmon management is to be based? No single perfect method has been devised, but well-designed surveys to address a wide array of the public's values (not just economic concerns of special interests) are an important tool. More such surveys are needed in guiding our salmon and other resource management. It is to be hoped that we are entering what Wilson (1984) called the "third" phase, where values — not just random technologies or short term economics — once again become important.

Perspectives on Pacific Salmon Management

Management under Uncertainty

Research and detailed knowledge of a particular natural salmon stock are not needed for the stock to be managed well, as long as harvest is moderate. In general, the more intense the harvest, the greater the need for quickly available, accurate information. Most problems with management in North America have not been because of lack of data. Mundie (1977) said it succinctly: "Inadequate knowledge of the ecological needs of the salmon has not been a prime cause of their decline. Decisions have been made knowingly." Under intense harvest situations such as those for salmon in the Pacific Northwest, research may provide the information to fine-tune our knowledge of stock distributions, develop management measures, and perhaps increase production, but no amount of research will compensate for overharvest of stocks or poor habitat management. Just as science is no substitute for values, good research is no substitute for poor management. It has long been accepted that good research leads to better management, but it is less well recognized that, in salmon, good management leads to better research. If the management framework is sound, data collection is facilitated, and more scientific knowledge follows (Silvert 1978).

In the common property salmon fisheries of the Pacific Northwest, self-interest economics and "tragedy of the commons" behavior from commercial, tribal, and recreational fishers often lead to the harvest of every fish even suspected (however unrealistically) of being "surplus" to the needs of escapement. The long-term maintenance of the fish stocks, rather than short-term benefits to harvesters, must begin to receive the benefit of the doubt (Wright 1981).

Who Should Manage the Public's Salmon?

It is ironic that the construction of dams and other technological projects harmful to salmon have funded and inspired most problem-solving technologies such as hatchery production. Dam construction and other such industrial developments on the Columbia River, often decried by biologists, now provide the revenue, both directly through research and management funds and indirectly through taxes, to finance much of the ongoing research and management. Even more ironically, much of this power-generated funding is administered by the Bonneville Power Administration and disbursed by its own cadre of administrators to other federal agencies, states, and private consultants. Many state salmon biologists voicing opposition to dam construction and related technological development harmful to salmon thus find themselves in the awkward position of "biting the hand that feeds them." The situation is similar, but less extreme, in other places in the Pacific Northwest. On the Columbia River, the fox does not merely guard the henhouse, he *owns* it. Clearly, management of salmon in nearly all Pacific Northwest rivers must occur as part of a broader multiple use plan encompassing hydropower development, irrigation, forestry, and other activities. However, there should be movement toward insulating biologists from direct financial control by Bonneville Power Administration contracting officers and other nonagency special interests. Funding from the power generation activities should not be restricted to contracts, but should also include guaranteed grants, with no hydroelectric strings attached, to state agencies charged with managing salmon. Since the salmon paid for the hydropower and other developments, their managers should have a clear voice when defending the interests of salmon.

Specialists and Generalists in Salmon Management

In the Pacific Northwest, where several different value systems vie continually for management authority, regulations are complex and man-made uses and alterations of ecosystems are many, and specialists abound. For harvest, there are specialists in salmon data analysis and salmon stock modeling. The proliferation of hatcheries for mitigation, for enhancement, and for food has led to much research by specialists in narrow segments of reproductive physiology (induced maturation, control of sex

ratios, induced sterility, stress), fish diseases (bacterial, viral, parasites, vaccines), nutrition (diets, feeding regimes), genetics (brood-stock development, selective breeding) — research in a host of highly specialized subfields populated, for the most part, by highly specialized scientists.

These specialists often develop technologies with little consideration of their effects on management. For example, at the 1983 International Symposium on Salmonid Reproduction, a paper was presented by E. M. Donaldson and G. Hunter entitled "Sex control in Pacific salmon: implications for aquaculture and resource management." The authors presented evidence that their artificially sterilized salmon, once released to the ocean, "do not undergo an anadromous migration but remain in the fishery and continue to grow." Their coded-wire tagged salmon were to be caught at sea several years later and at much larger sizes than would have occurred in maturing salmon. They noted that production of sterile salmon would benefit the aquaculturist because the salmon do not undergo maturation and the associated loss of market acceptance that results from poor flesh quality. They went still further in describing the management applications: "Sterile fish also present significant options for fisheries management... the production of sterile fish is a means of redistributing fish from fisheries of low value to fisheries of high value, i.e., from terminal harvest to ocean harvest."

They did not consider the desirability of having millions of larger than normal salmon remaining in the ocean instead of returning to natal streams or hatcheries. Nor did they consider the potential effects of thee large fish on wild smolts — predation on them and competition with them for food. In addition, the effects on other species and community structure were not mentioned. Perhaps most importantly, it is unclear how wild salmon stocks respond to the higher oceanic harvest rates associated with harvesting these sterile fish. With our increasing knowledge of the stock concept and the apparent long-term ecological rationality of harvesting on a stock-specific basis, we must ask if we want to expand our oceanic harvest of salmon.

Managers now have the option of producing sterile salmon, and they must interpret societal values and decide whether or not to produce them, or at least to decide whether to encourage or discourage their use, for example, at hearings of state commissions or of Federal Fishery Management Councils. But the mere discovery of an option must never guarantee its use. Managers must evaluate the particular technological option in the context of the management plan.

Although highly skilled specialists (e.g. good researchers in specific areas) can be vital in developing new technologies and solving many of our fisheries problems, the generalists (e.g. good fishery managers) must keep them in their place. Generalists attempt to understand ecosystems and value systems; specialists attempt to solve specific problems. A generalist either finds a natural ecosystem to investigate (e.g. a natural salmon river) or chooses or is forced to work with man-altered ones. A specialist usually responds to problems created by other specialists. Someone will build a dam, someone will then try to culture fish for mitigation and then have disease or maturation problems, and so on, much like Dr. Seuss' "Cat-in-the-Hat," where more technology is needed to meet the emergencies that technology itself has produced (Grant 1986). In the words of Wendell Berry (1977): "Because by definition, they lack any sense of mutuality or wholeness, our specializations subsist on conflict with one another.... The *problem* thus becomes the stock in trade of specialists" (italics added). For generalists, the emphasis is often ecological; for the specialist, technological. Only the generalist with an ecosystem and cultural perspective is qualified to evaluate these specialists and to be a successful salmon manager. Even if this person is just one of a committee that evaluates the technological discoveries of specialists, he must be cognizant of ecosystems and values.

Ocean Fishing for Salmon and Its Consequences

Many of the problems with current salmon management in the Pacific Northwest center squarely around the evolution of preemptive offshore fishing. Although additional problems have developed regarding the inadequate regulation of private salmon ranching (Shupe 1982) and inriver allocations, these and other problems are more manageable than the question of ocean fishing.

In the Pacific Northwest, there is an extensive history of offshore interceptions that have impeded stock-specific management of salmon (Larkin 1970, 1979, 1980). The interceptions occur internationally (United States, Canada, Japan, Soviet Union) and also between states (California, Oregon, Washington, and Alaska). As more efficient terminal in-river gears were successively outlawed (Smith 1974), the offshore fishery expanded. As wild stocks diminished from habitat destruction and mixed-stock overfishing, the production of hatchery fish rose, until today, commercial and recreational troll fisheries constitute the primary harvesters of salmon in many regions of northwestern United States, and much of their harvest is hatchery-reared fish (Oregon Department of Fish and Wildlife 1982b), paid for by the public.

The proliferation of common property oceanic commercial and recreational salmon fisheries, mostly by nonfarmers and others not closely tied to the land, has divorced the salmon from the land and from the rivers and thereby reduced the possibility of an ecologically oriented North American land ethic benefitting salmon. According to Aldo Leopold (1970), "a land ethic... reflects the existence of an ecological conscience, and... a conviction of individual responsibility for the health of the land." With oceanic harvest by commercial and recreational fishers, harvest has been isolated from land and river stewardship, and the salmon is viewed as a nomad owned by whomever catches it. If the abundance of stocks and yields to offshore fisheries are low, oceanic fisheries blame the managers and the inland people for abusing the rivers and the lands around them. And since these oceanic fisheries have all persisted, to varying degrees, on mixed stocks, some smaller stocks and substocks have almost certainly been exterminated before they were even identified by biologists. An ecologically based North American land ethic (Leopold 1970), although well articulated in books, has thus been largely ineffective in protecting and conserving salmon in the Pacific Northwest.

However, steelhead (*Salmo gairdneri*), which have been designated a game fish and thus not harvestable commercially by non-Indians, and are not often caught at sea anyway, have gained the benefits of a land ethic. In the northwest, the salmon–land linkage persists most strongly, of course, in inland commercial, subsistence, and recreational users — land-linked groups such as Indian tribes and conservation groups such as "Oregon Trout." With land-based salmon management, the linkage has been maintained between wise land and river management and the rewards of harvest.

Before the passage of the *Magnuson Fishery Conservation and Management Act* of 1976, interceptions of salmon between

states and countries in the Pacific were largely unregulated except for salmon stocks covered by international fisheries agreements such as the International Pacific Salmon Fisheries Commission (IPSFC) and the International North Pacific Fisheries Commission (INPFC). In the United States before the mid-1970s, most ocean salmon management outside 3 miles, and virtually all management inside 3 miles, was done by states. With the passage of the *Magnuson Act*, the powers of the U.S. federal government expanded greatly; they assumed primary responsibility for management outside 3 miles, and could even preempt state management authority inside 3 miles if state actions were deemed inconsistent with federal management (Severance and Bubier 1985).

Each of these international agreements and the *Magnuson Act* have led to some stability in the interceptions of salmon, and undoubtedly prevented some extinctions of stocks. In addition, insightful research by the IPSFC and the INPFC has expanded our knowledge of many aspects of the salmons' life histories. However, the long-term effects of these organizations on the salmon stocks are less clear. Since none of the agreements were signed nor the *Magnuson Act* enacted to eliminate ocean fishing, it is not surprising that both the ocean fishing and most of the commissions (or their successors) and the regional Fishery Management Councils are still managing salmon. Most biologists agree that with the existence of oceanic salmon fisheries, the most logical management entity is the federal government. Even the regional Councils cannot adequately address international salmon interceptions (hence the need for the U.S.–Canada treaty). Clearly, no state can possibly address the oceanic harvest and allocation problems alone. Because of the obvious complexities associated with managing mixed stocks of highly migratory salmon at sea, there have been consistent needs and calls for more and more federal authority in U.S. salmon management (Berg 1981). The questions raised here are not whether the federal government should or should not now be involved in salmon management, but in what capacity, and if their powers should be increasing.

The federal government, acting through the Councils, is inherently best able to manage common property fisheries for true ocean species — especially migratory species inside the Fishery Conservation Zone that are not directly linked to the land and can get no protection from a land ethic or from states. But salmon — land-linked species composed of many distinct local stocks — do not fit this description well. Only a very few aspects of ecologically sound salmon management call for federal action. Most aspects of federal salmon management are justified politically and socially rather than ecologically.

As it now stands, preemptive oceanic commercial and recreational fishing for salmon and the Pacific and North Pacific Fishery Management Councils are solutions to each other's problems — the federally funded Councils institutionalize and stabilize the ocean fisheries, preventing rampant overharvest, at least of major stocks or those minor ones involved with treaty obligations. Without the Councils, common property chaos and "balkanized" (Berg 1981) management would lead to overharvest and destruction of the industry. This federal management is highly centralized, energy consumptive (human and otherwise), expensive, and frequently out of touch. It is no exaggeration to say that Council members, Salmon Advisory Subpanels members, and Salmon Plan Development Team members are sometimes making important management decisions in a far-distant hotel conference room for salmon rivers that they have never seen. It is not entirely their fault; under centralized harvest management of oceanic fisheries, it might take years to see all rivers involved in important harvest decisions. Such managers, although often of high innate intelligence, must struggle continuously to stay in touch with the rivers, the land, the salmon, and the human users. In the meantime, land-based salmon stewardship is reduced or preempted.

It is worth asking the public if Pacific Northwest salmon management should be moving, even if gradually, to greatly reduce or even eventually eliminate these oceanic fisheries, rather than merely institutionalizing them. A gradual phase-out or phase-down of these subsidized fisheries would lessen immediate economic hardships on coastal user groups, who have in recent years been inordinately benefitting from the public's (including inland citizens') salmon resources. Without the ocean fisheries, the need for federal involvement would then be restricted to issues such as international fishing treaties, salmon ranching regulations, acid rain effects, certain tribal issues, and other such issues best dealt with at that level. Most aspects of the land- and river-based salmon management could be conducted more ecologically and at lower cost by interstate agreement, and by state and local managers. And with the development of pen-rearing technologies for salmon in North America and abroad, steady supplies of salmon are now becoming available all months of the year. The advantages of terminal management and terminal harvest of stocks will become more evident as oil and gas supplies decline in the mid-1990s, making even the short-term economic rationale for oceanic fisheries less attractive.

However, the state and local managers would need to be insulated from short-term economic pressures of special interests much more effectively than in the past. For example, salmon ranchers have frequently supported reduction or elimination of offshore fisheries, not so much from concern for the plight of wild stocks, but to reduce oceanic harvest rates on their ranched fish. State and local managers would need the autonomy to make decisions based on information about wide-spread public values rather than the short-term economic demands of any of these user groups. The historical inability of states to cope with these special interests is one factor that led to federal management in the first place.

Perhaps in the future, ecologically sound management of salmon will evolve so that less, not more, federal authority is needed. It seems almost a law that oceanic fishing for mixed stocks of salmon, wherever and whenever begun, is never halted by managers — it is just institutionalized and controlled. Perhaps it is time to view oceanic commercial and recreational salmon fishers, salmon ranchers, and other special interests as instruments of the public's values and policies, rather than as mouths that the public's natural, technological, and energy resources must feed at all costs. Oceanic fishing and salmon ranching might then be seen properly as a *privilege* granted by the public and supervised by the manager, not a guaranteed *right* of any one person to profit at the public's expense.

If more salmon would come back to the Northwest rivers, local residents would be more effective in their stewardship and more enthusiastic about the management of their rivers. They could also keep meaningful long-term records on the salmon of their rivers and provide biologists valuable site-specific information for management (like steelhead anglers often do). Salmon biologists could also be biologists — working, at least sometimes, in waders in rivers, and not always seen in three-piece suits in hotel lobbies, rental cars, and airports. Middle layers of bureaucracy would be reduced. The manager making

most of the important decisions on the river and stocks would be the one most familiar with the river and the salmon, and most able to learn and interpret the values of the culture through a balance of outside education and local inside knowledge. Within the ecologically sound centralized framework for local management, many different management plans could evolve for different rivers, each a unique work of art with science as its method, and the persistence of the stocks and the accompanying wise human use as its goal. Some existing positions and programs in the Northwest have these essential characteristics. The District or Regional biologist is one such position from which agencies can foster land and river stewardship. In addition, public participation programs such as the Oregon Department of Fish and Wildlife's Salmon and Steelhead Enhancement Program (STEP) are encouraging land and river stewardship. Similar programs emphasizing long-term stewardship rather than short-term harvest should be expanded and promoted.

The Future of Salmon Management

> The shallow-minded modern who has lost his rootage in the land assumes that he has already discovered what is important. It is only the scholar who appreciates that all history consists of successive excursions from a single starting point, to which man returns again and again to organize yet another search for a durable scale of values.
>
> —Aldo Leopold, *Wilderness*

In the last two chapters of "The Firmament of Time," the paleontologist Loren Eiseley (1960) asks peole to recognize the distinction between advances in scientific knowledge and improvement in man himself. In his words: "Science is not enough for man.... We fallaciously equate ethical advance with scientific progress in a point-to-point relationship."

Humanity's unprecedented technological progress carries with it a great responsibility — we must consciously, willfully decide how to use our discoveries to attain and embody our values. For natural resource managers, this responsibility becomes even more critical as the rate of new technological discoveries accelerates and as these technologies enable us to produce large-scale changes in ecosystems. Yet amidst the deluge of narrowly defined technical papers published on salmon biology and management, papers on the philosophy of salmon management have been scarce. Perhaps the technical demands of biologist's jobs are so great that biologists have no time to develop and articulate philosophies of management. Perhaps our researchers and managers are uncomfortable with philosophy and believe that their roles as objective scientists are compromised by taking philosophical stands on issues. Perhaps in these days of reduced job availability, biologists fear for their financial security and avoid dealing with difficult, awkward political and ethical questions. Or pehaps, as one biologist once told me, fishery management, including salmon management, deserves no special attention in philosophy. As R. D. Hume (1893), an early salmon fishery entrepreneur and hatchery advocate, put it: "The salmon industry of the Pacific Coast has been both directly and indirectly the means by which very many have made fortunes, and who without its benefits would perhaps find themelves out of employment and lighter of pocket." Maybe the complex management system in the Pacific Northwest, with its oceanic fishers, its in-river commercial and tribal interests, its anglers, its culturists and salmon ranchers, its fishery managers, biologists, and technicians, countless administrators and attorneys assembled in committees and working groups, and its multitudes of dam builders and dam mitigators, is just the end product of a growth-oriented, technologically driven society designed and perpetuated to keep everyone, including biologists, employed, off welfare, seeking technologically stimulating solutions to specialized problems created by someone else's technology. Many highly trained people are required to develop and maintain a technological infrastructure, and all these people must be kept busy doing *something*. It may thus be an illusion to suggest that our objective in salmon management is to simplify and reduce the cost of harvest, harvest management, or mitigation and enhancement while creating an ecologically rational and energetically prudent system of salmon management. Maybe this artificially complex, positive-feedback technological society we have created is our destiny, both our means and our end, and this is where society's values lie after all. The tragedy is that 100 yr after Hume, our dwindling natural resources, including the salmon, are still paying a high price for, rather than benefitting from, so many of our experiments with technologies.

In one of the rare articles discussing philosophical aspects of salmon management, Larkin (1980) wrote: "I don't fancy myself as an economist, political scientist, social scientist, or *philosopher*" (italics added). Yet to be an effective salmon manager is to be both a student and a teacher of fishery science, of philosophy, and of human values. The actions of a fishery manager perforce transcend objective science, random application of technology, and moral absolution for actions taken. It is to be hoped that new generations of salmon managers develop and articulate their values and philosophies more clearly than the present generation has done, and that the new generations investigate the public's values and inform the public about values as well. As human demands on the salmon and their habitats inexorably mount, the need for values becomes more and more urgent.

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ANNOUNCEMENTS/AVIS

13th Annual Meeting
American Fisheries Society
Early Life History Section

May 21–27, 1988
Merida, Yucatan, Mexico

The theme is Larval Fish Recruitment and Research in the Americas. There will be three days of presented papers and two days of workshops, including a special workshop on the order Scombroidei. Field trips include a visit to the Mayan Ruins at Uxmal and diving at Isla Mujeres.

For more information, contact Andrea Frank, Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 34236, USA. Telephone: (813) 388-4441.

Second Conference of the International Federation of Classification Societies (IFCS)

June 27–30, 1989, Charlottesville, VA

The conference is devoted to the presentation of theoretical, methodological, and applied papers on classification, pattern recognition, and related methods of statistics and data analysis in the broad sense. Papers are invited for this meeting.

If you plan to attend the conference or have general inquires about the conference, write to IFCS–89, Department of Mathematics, University of Virginia, Charlottesville, VA 22903, USA. Telephone: (804) 924-4919; Bitnet: SJT@VIRGINIA.

If you plan to present a paper, send an English abstract of at most one page to Robert F. Ling, Chairman, IFCS-89 Program Committee, Department of Mathematical Sciences, Clemson University, Clemson, SC 29634–1907, USA. Bitnet: RFLING@CLEMSON. Deadline for submitting papers is January 15, 1989.

Treizième réunion annuelle
American Fisheries Society
Early Life History Section

21 au 27 mai 1988
Merida, Yucatan, Mexique

La réunion aura pour thème le recrutement larvaire des poissons et la recherche dans les Amériques. La présentation de communications durera trois jours et les ateliers deux jours. Un atelier spécial sur l'ordre des scombroidés sera aussi tenu. Les sorties prévues comprennent une visite du site maya de Uxmal et de la plongée sous-marine à Isla Mujeres.

Pour plus de détails, veuillez entrer en relation avec Andrea Frank, Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 34236, USA. Téléphone : (813) 388-4441.

Deuxième conférence de la Fédération internationale des sociétés de classification (FISC)

27 au 30 juin 1989, Charlottesville, VA

Cette conférence est consacrée à la présentation d'exposés théoriques, méthodologiques et appliqués concernant la classification, la reconnaissance de formes et des méthodes connexes de statistiques et d'analyses des données en général. On invite les personnes intéressées à présenter des exposés à cette conférence.

Pour des réservations ou des informations supplémentaires concernant la conférence, écrire à l'adresse suivante : IFCS-89, Department of Mathematics, University of Virginia, Charlottesville, VA 22903, USA. Téléphone : (804) 924-4919; Bitnet : SJT @ VIRGINIA.

Si vous souhaitez présenter un exposé, envoyer un résumé en anglais d'au moins une page à : Robert F. Ling, Chairman, IFCS-89 Program Commmittee, Department of Mathematical Sciences, Clemson University, Clemson, SC 29634-1907, USA. Bitnet : RFLING @ CLEMSON. La date limite pour la présentation des mémoires est le 15 janvier 1989.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

King, J. M., J. A. Day, P. R. Hurly, M-P. Henshall-Howard, and B. R. Davies. Macroinvertebrate communities and environment in a southern African mountain stream

Petrosky, C. E., and T. C. Bjornn. Response of wild rainbow (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) to stocked rainbow trout in fertile and infertile streams

McQuinn, I. H., L. Gendron, and J. H. Himmelman. Area of attraction and effective area fished by a whelk (*Buccinum undatum*) trap under variable conditions

Andrus, C. W., B. A. Long, and H. A. Froehlich. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging

Ennis, G. P., R. G. Hooper, and D. M. Taylor. Functional maturity in small male snow crabs (*Chionoecetes opilio*)

Grewe, P. M., and P. D. N. Hebert. Mitochondrial DNA diversity among broodstocks of the lake trout, *Salvelinus namaycush*

Hall, R. J., R. C. Bailey, and J. Findeis. Factors affecting survival and cation concentration in the blackflies *Prosimulium fuscum/mixtum* and the mayfly *Leptophlebia cupida* during spring snowmelt

Hinch, S. G., and R. H. Green. Shell etching on clams from low-alkalinity Ontario lakes: a physical or chemical process?

Forster, I., D. A. Higgs, G. R. Bell, B. S. Dosanjh, and B. E. March. Effect of diets containing herring oils oxidized to different degrees on growth and immunocompetence of juvenile coho salmon (*Oncorhynchus kisutch*)

Erman, D. C., E. D. Andrews, and M. Yoder-Williams. Effects of winter floods on fishes in the Sierra Nevada

McIsaac, D. O., and T. P. Quinn. Evidence for a hereditary component in homing behavior of chinook salmon (*Oncorhynchus tshawytscha*)

Cunjak, R. A. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter

Lathrop, R. C. Evaluation of whole-lake nitrogen fertilization for controlling blue-green algal blooms in a hypereutrophic lake

Arts, M. T., and W. G. Sprules. Evidence for indirect effects of fish predation on maternal lipid allocation in *Holopedium gibberum*

Metcalfe, C. D., V. W. Cairns, and J. D. Fitzsimons. Experimental induction of liver tumours in rainbow trout (*Salmo gairdneri*) by contaminated sediment from Hamilton Harbour, Ontario

Yamamori, K., M. Nakamura, T. Matsui, and T. J. Hara. Gustatory responses to tetrodotoxin and saxitoxin in fish: a possible mechanism for avoiding marine toxins

Spry, D. J., and C. M. Wood. Zinc influx across the isolated, perfused head preparation of the rainbow trout (*Salmo gairdneri*) in hard and soft water

Starr, P., and R. Hilborn. Reconstruction of harvest rates and stock contribution in gauntlet salmon fisheries: application to British Columbia and Washington sockeye (*Oncorhynchus nerka*)

Subba Rao, D. V., M. A. Quilliam, and R. Pocklington. Domoic acid — a neurotoxic amino acid produced by the marine diatom *Nitzschia pungens* in culture

Tarapchak, S. J., and L. R. Herche. Orthophosphate concentrations in lake water: analysis of Rigler's radiobioassay method

Johnson, L. L., E. Casillas, T. K. Collier, B. B. McCain, and U. Varanasi. Contaminant effects on ovarian development in English sole (*Parophrys vetulus*) from Puget Sound, Washington

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